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Estimating weaning and early childhood diet from serial micro-samples of dentin collagen

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ABSTRACT

Age of weaning is an important measure of parental investment, and in various human and non-human primate studies, has been correlated with a range of developmental factors such as stature, cognitive functions, obesity, ability to cope with stress, and rates of disease. Archaeological estimation of the weaning process is generally at the level of an entire burial population, creating some challenges in using such data to test anthropological theory. We describe a method that tracks the weaning process at the individual level, based on the measurement of stable nitrogen and carbon isotope ratios in serial sections of first molar dentin collagen. We apply this micro-sampling technique to a sample of individuals from CA-CCO-548, a well-studied and ancient site on the banks of Marsh Creek in Central California. Results show great variation between individuals in both the length of the weaning process, the age at which breastfeeding stopped, and the source of early complementary childhood foods.

1. Introduction

Humans pursue a wide range of mating and reproductive strategies that pit trade-offs between maximizing the number of offspring and ensuring specific offspring will survive to reproduce themselves (e.g., Blurton-Jones, 1986; Borgerhoff-Mulder, 1992, 2001; Kaplan, 1996; Stearns, 1992; Trivers, 1974). These trade-offs are, of course, embedded within cultural systems with rules about behavior that can either promote or inhibit reproductive and parental investment practices.

The age at which a mother weans a child is a strong measure of parental investment in offspring among primates, including humans (Stuart-Macadam and Dettwyler, 1995). Breastmilk provides an offspring a reliable and easily digestible source of calories and nutrients and contains important antibodies, but on the other hand, its production is a significant energetic investment and reduces the fertility of the mother (e.g., Borgerhoff-Mulder, 1992; Delgado et al., 1982; Riordan, 2005; Sellen, 2006). Studies in modern populations suggest that the duration of breastfeeding is correlated positively with stature and later cognitive functions (e.g., IQ) and negatively with obesity and rates of some immune-related diseases, among other benefits (e.g., Mortensen et al., 2002; Schack-Nielsen and Michaelsen, 2006; Taren and Chen, 1993). Mothers may be aware of some of these effects, at least at a general level, as some studies suggest that mothers alter the age of weaning depending on individual attributes of a child (e.g., underweight children are breastfed longer; see Martin, 2001; Sellen and Smay, 2001; Simondon et al., 2001). Likewise, recent studies with macaques show that increased levels of breastmilk during the early years have long-term effects on offspring confidence and the ability to cope with stress (Hinde and Capitanio, 2010; Hinde et al., 2009). Together, these studies demonstrate the value of longer breastfeeding and increased parental investment in the survival and fitness of offspring. In the evolution of mammals and humans, such benefits must have greatly outweighed the energetic and fertility costs to females.

For these reasons, measuring variation in the age of weaning is of great interest to anthropologists and archaeologists (Sellen and Smay, 2001). For example, behavioral ecological models make predictions about age of weaning relative to environmental risk. In a test of the model, Quinlan (2007) shows that maternal investment in offspring varies inversely with rates of famine and warfare within a range of modern societies. More specifically, he found that age of weaning shows strong relationships with pathogen stress, where low and high rates of disease are correlated with earlier weaning, and moderate pathogen stress with the highest average age of weaning. Likewise, Humphrey (2010) argues that shifts in weaning reflect changes in the balance between the costs of lactation, the risk of child mortality, and nutritional and metabolic

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requirements of offspring. She argues that the increasing size of Neanderthal and archaic modern human brains slowed maturity and led to a delayed onset and early cessation of reproduction. Such changes would have reduced the reproductive lifespan of females, which may have selected for a decrease in the average age of weaning.

Archaeological samples have an important role to play in the debates about variation and changes in the age of weaning among humans. Such studies would greatly broaden the diversity of cultural groups represented, providing a more robust test of various ecological models. Furthermore, archaeological samples are the only means to reconstruct long-term evolutionary trajectories in weaning behavior. In this respect, developing methods to estimate age of weaning in ancient populations or individuals is an important goal. We define weaning as a process, marked by an initial period of exclusive suckling, a period of declining breastfeeding (milk consumption) and increasing consumption of complementary foods, and finally, termination of breastfeeding altogether (Lewis, 2007:99; McDade, 2001:10). However, humans are notoriously variable in both the length of time different phases encompass and the details of how they are implemented, for example, in the source of complementary foods (Sellen, 2006).

2. Reconstructing age of weaning in archaeological samples

Generally, there are two approaches to reconstructing the weaning process in the bioarchaeological literature, both relying on geochemical data. Both approaches rest on the notion that there is a trophic-level effect on isotope or element fractionation between mother and infant, where a breastfeeding infant is expected to be enriched or depleted in a particular measure relative to the mother. This effect has been shown to occur for stable nitrogen and/or oxygen isotopes (Fogel et al., 1989; Fuller et al., 2006a; Wright and Schwarcz, 1998, 1999) and has been argued to hold for the element strontium, generally as a ratio of calcium (e.g., Katzenberg, 1992; Katzenberg et al., 1996; Mays, 2003; Sillen and Smith, 1984). During the weaning process, as a child is transitioned onto complementary liquid or solid food, δ^{15}N and δ^{18}O isotope or Sr/Ca ratios transition to "normal" adult levels.

In archaeological applications, stable δ^{15}N isotopes of bone collagen taken from individuals who died at various ages, estimated based on other factors such as dental development, tooth eruption, diaphyseal length and epiphyseal fusion, are plotted against one another for the entire population. Generally, a pattern emerges where young individuals (e.g., 0–3 years) are elevated in the heavier ^{15}N with progressively older individuals showing transitional or more adult δ^{15}N values (Choy et al., 2010; Clayton et al., 2006; Fuller et al., 2006b; Gardner et al., 2011; Herring et al., 1998; Katzenberg and Pfeiffer, 1995; Pearson et al., 2010; Schurr, 1997; Schurr and Powell, 2005). Mays (2003) found a very similar pattern for Sr/Ca ratios from the Medieval cemetery population from Wharram Percy, England, showing increasing Sr/Ca ratios with age at death during the weaning process.

Such cross-sectional approaches reconstruct the average age of weaning in a burial population. As well, they allow archaeologists to see the entire modal weaning process, from the initial introduction of complementary foods to the cessation of breastmilk altogether. Comparing populations from different points in time or space can provide important information about variation in breastfeeding behavior, related to environment, culture history, or other factors. Furthermore, because breastfeeding affects female fertility (e.g., Riordan, 2005), this measure is an important tracer on one of the causes (or byproducts) of population growth (e.g., Crown and Wills, 1995). As mentioned, human behavioral ecological theory predicts that the age of weaning should vary across populations in relation to environmental or social risks. In this respect, archaeological data can play a crucial role in testing such theory.

There are also drawbacks to this approach. First, because age of weaning is averaged across many individuals in a burial population, it is difficult to examine intra-population variation in the age of weaning. Infants and young children lack the diagnostic attributes to determine sex and have not lived long enough to accumulate significant material wealth. Lacking such information, we cannot test whether there is greater investment in, for example, females versus males, low versus high status, or tall versus short individuals. Second, because temporal control is imprecise, archaeological "populations" often represent the accumulation of individuals over centuries. Grouping such samples into a single population may mask more fine-scaled changes in weaning behavior in response to short-term social and environmental variations. Third, dietary changes (e.g., cessation of breastmilk, introduction of complementary foods) are not immediately recorded in bone due to remodeling, making it difficult to precisely estimate the age at weaning (Lewis, 2007). That is, some fraction of the collagen analyzed will represent bone that formed in the more distant past, not close to the time of death. Correcting for this delay due to remodeling is difficult because the magnitude of the effect varies with age (see Hedges et al., 2007), with faster bone turnover rates in infancy compared to early childhood. Because teeth do not remodel, they do not display this effect. Fourth, it is unclear whether infants and young children in archaeological samples represent "average" or typical individuals. For example, such individuals may have died early because they were weaned early. Alternatively, they may have been sickly individuals who were expressly breastfed longer than the average (e.g., Simondon et al., 2001). In sum, although certainly a good first approximation of the weaning process within a group, the cross-sectional or population level approach has some interpretive challenges when testing anthropological theory.

An alternative approach focuses on estimating the age of weaning and other life history information for individuals, rather than populations (e.g., Sealy et al., 1995). This approach has been applied less often and generally involves measuring the breastfeeding signal across different teeth from a single individual. Because different teeth form at different ages, and unlike bone, do not remodel after they are formed, relative differences between teeth can indicate the approximate age at which an individual was weaned. For example, Dupras and Tocheri (2007) used δ^{13}C and δ^{18}O isotopes from enamel and δ^{13}C and δ^{15}N isotopes from dentin using different teeth (e.g., incisors, canines, premolars, and first, second, and third molars) to estimate ages of weaning. Although they could have examined individual level differences in the age of weaning, among for example males and females, they pooled the data to focus on weaning practices at the population level. Their study did, however, circumvent the fourth issue mentioned above. Thus, their study included individuals who survived the weaning process and did not die prematurely because they were weaned early.

More to the point, Wright and Schwarcz (1998) measured δ^{13}C and δ^{18}O isotopes in the phosphate component of enamel of a first molar, a premolar, and a third molar of the same individual. They repeat the analysis for a sample of 35 individuals from a Maya burial population. Results show consistent differences, especially in δ^{18}O which becomes heavier across these three teeth, which they interpret as a byproduct of the weaning process. Their study improved on earlier approaches, allowing Wright and Schwarcz to compare weaning in different segments of the population. One limitation was that only three "point" estimates of breastmilk input during the life of an individual were collected, one of which is almost certainly post-weaning in any individual (i.e., third molar). The small number of data points recording breastmilk input (effectively, $n = 2$), did not provide data at a fine-grained level to reconstruct weaning as a process. Furthermore, the approach requires the partial destruction of multiple teeth per individual.

In this study, we take an alternative approach. Rather than comparing different teeth, or estimating the average age of weaning within a population, we are interested in individual level differences in the weaning process. Our approach takes inspiration from that of Fuller et al. (2003), where teeth were sectioned into three parts (crown, cervical, and apical section), with dentin collagen extracted from each and measured for $\delta^{15}N$ and $\delta^{13}C$ isotopes. The Fuller et al. methodology hinges on the fact that dentin grows sequentially from the crown to the root tip over time, and that the tissues deposited are not subsequently remodeled or otherwise altered during the course of an individual's life. Although Fuller and colleagues were still only able to generate three point estimates of breastmilk input for an individual, their approach minimized sample destruction to the dentin of a single tooth, and also allowed them to compare different segments of a population.

Our approach is similar to that of Fuller et al. (2003) except that we cut the dentin of first molars into much smaller sections allowing us to make many more estimates of diet throughout the development of the tooth. We were able to sample between 5 and 10 serial sections per tooth, giving much greater temporal control over diet. First molars begin growing at the time of birth (age = 0) at the dentino-enamel junction (DEJ), the crown is typically complete by 2.5–3 years of age at the cementum–enamel junction (CEJ), and the apical root tip closes around age 9–10 (Hillson, 1996). There is little difference in the timing of growth between upper and lower or left versus right first molars.

This sampling strategy gives us the same types of weaning curves seen in the population level studies (e.g., Choy et al., 2010; Clayton et al., 2006; Fuller et al., 2006a,b; Gardner et al., 2011; Katzenberg and Pfeiffer, 1995; Mays, 2003; Schurr, 1997), but at the individual rather than the population level. Provided that enough of the tooth is preserved, a single first molar can be used to reconstruct the entire weaning process, as it records diet from infancy into childhood up to approximately age 9–10. This facilitates comparison of age at weaning against measures of health (e.g., stature, enamel hypoplasia), sex, and status, among others, for individuals within a population. Such micro-sampling combined with stable isotope analysis has been applied to dental tissues of animals (e.g., Balasse and Tresset, 2002; Balasse et al., 2001; Zazzo et al., 2006; Humphrey et al., 2008a, 2008b; Kirsanow et al., 2008), but to our knowledge has only recently been applied to human teeth (Burt and Garvie-Lok, 2011).

3. Sample and methods

This study attempts to reconstruct the age of weaning for six individuals from the Marsh Creek Site (CA-CCO-548). This site lies on the western edge of the Sacramento-San Joaquin Delta in the Central Valley of California (see Fig. 1). The site is situated on the banks of Marsh Creek (freshwater), which flows east and then north into the lower reaches of the delta. The fresh to brackish water delta is inter-connected by a series of meandering sloughs to the San Francisco Bay estuary. The delta and its inflowing tributaries provided access to a range of aquatic resources including anadromous fish (e.g., salmon, sturgeon) and migratory waterfowl (Schoenherr, 1992). Some low trophic level and protein-rich resources (e.g., shellfish, crabs) were available along the ecotone of the estuary and delta.

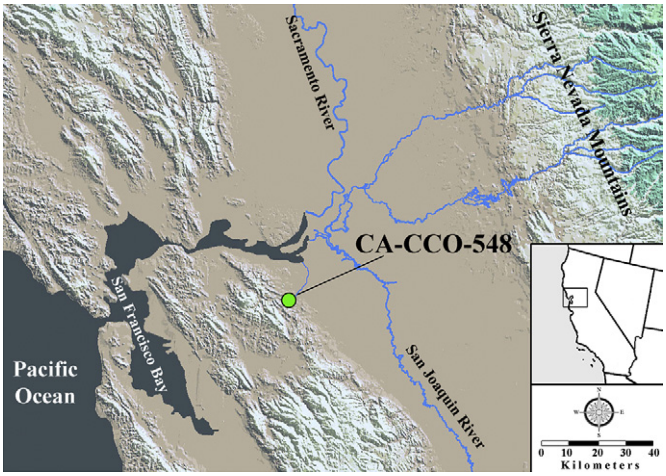

Fig. 1. Location of CA-CCO-548 in Central California.

CCO-548 was excavated in several phases between 2003 and 2008 for a housing development, resulting in the excavation of approximately 480 burials (Wiberg, 2010). Although there is both earlier and later occupational debris at the site, radiocarbon dating and temporally diagnostic artifacts place the cemetery component squarely in the Middle to Late Holocene, between approximately 4300 and 3100 BP. Prior to reburial, the Most Likely Descendant (a person assigned by the Native American Heritage Commission) provided permission for tooth and bone sampling for isotopic analyses.

In this study, we focus on analyses of first molars from five individuals, and a first-second-third molar sequence from a sixth individual. From the dentin component we extracted collagen for $\delta^{15}N$ and $\delta^{13}C$ stable isotope analysis to examine changes in early childhood diet, including weaning. For comparison, we also sampled a small fragment of bone from each individual, extracted collagen, and calculated $\delta^{15}N$ and $\delta^{13}C$ isotope ratios to establish an estimate of adult diet. Burials were dated either directly by radiocarbon means ($n = 4$) or by association with other radiocarbon-dated burials ($n = 2$). Table 1 lists the burials and associated demographic and isotopic information.

Because they are the first to erupt, first molars of adults are often highly worn in ancient populations. This is especially true in California which has some of the highest rates of occlusal attrition anywhere in the world (Jurmain, 1990). In many of the samples from CCO-548, much of the enamel and some of the underlying dentin within the crown have been lost to attrition. In a growing tooth, dentin begins forming at the DEJ and grows apically in successive layers toward the root. Due to the high attrition rates, some of the earliest dentin deposited (i.e., between age 0 and age 1) was often removed from the tooth, limiting our ability to reconstruct diet during the earliest stages of life. However, while some complementary food may have been consumed (e.g., acorn gruel) around six months, the protein component of the diet was likely composed primarily of breastmilk at this time.

For each tooth, we removed and saved any enamel for future and ongoing isotopic studies using a Foredom drill with a stainless steel bit. The remaining cementum and any exposed dentin was also completely drilled away to remove potential surface contaminants. The tooth was then rinsed in deionized water (DI), dried, and placed in dilute 0.5M HCl at 1 °C for demineralization. HCl was replaced every 1–2 days until the tooth no longer visibly reacted with the HCl solution and was spongy in texture (~5–10 days). Following demineralization, the tooth was rinsed and sliced with a scalpel into thin parallel sections approximately 1–2 mm thick, perpendicular to the central axis of the root. We are aware that these

Table 1
Burials included in this analysis, demographic information, and adult bone collagen C/N ratios, collagen yield, δ^{15}N, δ^{13}C, and uncalibrated radiocarbon age or age estimate.

Burial #	Sex	Age at Death	δ^{13}C (‰)	δ^{15}N (‰)	C/N Ratio	Collagen Yield (%)	^{14}C Age Uncalibrated	Median Calibrated ^{14}C Age BP
59	Male	25–35	−20.9	10.1	3.3	9.0	3010 ± 40	3135
79	Male	25–35	−19.6	9.9	3.5	2.0	3200–3000*	
87	Female	20–30	−19.6	9.3	3.3	6.0	3075 ± 25	3155
92	Male	30+	−19.5	9.8	3.3	2.0	3540 ± 25	3690
107	Male	35–45	−19.5	8.8	3.3	4.0	3505 ± 30	3650
275	Indet.	13–17	−19.7	8.6	3.3	6.0	3200–3000*	

Notes: Indet. = Indeterminate; * = Estimated ^{14}C age based on nearby radiocarbon-dated burials. Median calibrated radiocarbon age includes correction for marine component of diet.

sections cross the growth lines of dentin, especially in the root, and address this further below. Typically, we were able to generate between 5 and 10 serial sections per tooth, depending on the degree of tooth wear and the size of the tooth. Fig. 2 shows a hypothetical tooth and the general sampling methodology. In the figure, ten serial samples are shown from the root tip (labeled sample "A") to the crown (labeled "H"). Growth lines for the dentin were traced from an actual first molar showing the increasing angle toward the apex of the root, as well as the overlap between different serial sections of the root. In cases where collagen yield was low, we had to combine adjacent samples to introduce sufficient quantities of collagen for the mass spectrometer. Approximately 1 mg of collagen was needed for each stable carbon and nitrogen isotope analysis.

Table 2 presents information on the eight teeth included in this study, including the length in mm from the root tip to the CEJ and the distance from the CEJ to the occlusal surface (in most cases the DEJ had been partially or completely worn). The number of serial samples analyzed by mass spectrometry from each tooth is also shown.

Demineralized sections were then placed in separate glass vials, labeled, and treated with 0.125M NaOH for 24 h to remove humic contaminants. Samples were then rinsed with dH$_2$O, immersed in pH≈3 water, and placed in an oven at 80 °C for 24 h to solubilize the collagen. Samples were centrifuged, with the liquid fraction removed and freeze-dried. Collagen δ^{13}C and δ^{15}N was measured by continuous-flow mass spectrometry (PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer) at the Stable Isotope Facility at UC Davis. The atomic C/N ratio and the percent collagen yield are also reported in Table 2, and are useful indicators of sample quality (De Niro, 1985; van Klinken, 1999; Weber et al., 2005). Six of the eight teeth show adequate collagen yield (>2%) and C/N ratios between 2.9 and 3.6, both indicating good sample quality. Two teeth (burials 92 and 107) have one or more serial samples with C/N ratios above 3.6, and showed lower collagen yield values (ca. 1%). Radiocarbon dates show that both teeth are from the older burials at the site, thus age may partially explain the poor state of preservation. Samples with C/N values above 3.6 are highlighted in Fig. 3 with a heavy encircling black line. Higher C/N ratios indicate that either carbon is being added from outside the sample or nitrogen is being lost from within. Although the interpretation of these samples should be treated with caution, we believe δ^{15}N is still reliable because there is no indication that exotic N is being introduced to the teeth. Moreover, the serial samples with C/N ratios above 3.6 are still in line with other samples in the tooth, and did not produce unusually high or low δ^{15}N, and δ^{13}C values are not unusual either. In particular, serial samples from Burial 92 are especially elevated in C:N ratios, with four out of five above 3.6. As a result, we treat interpretation of the results of Burial 92 conservatively.

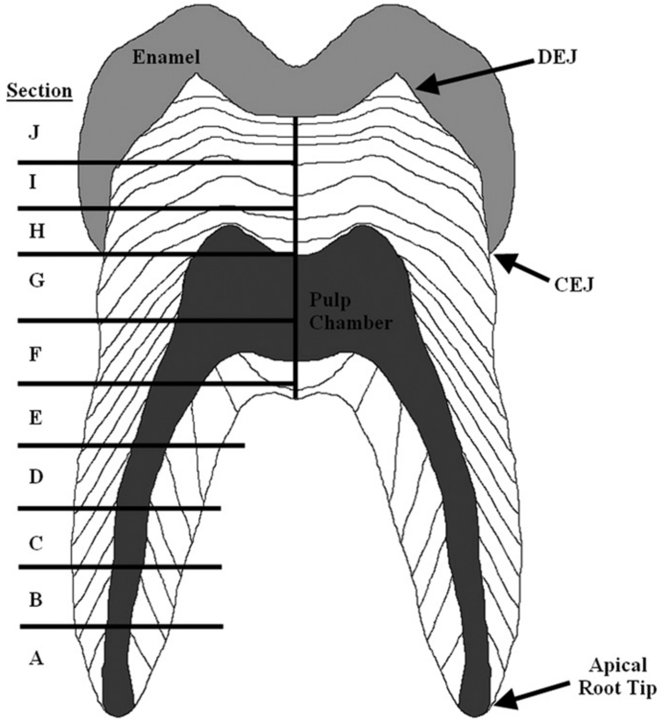

Fig. 2. Example of sampling strategy, with ten serial samples from root tip (A) to crown (J). Dentin in white, with approximate angles of growth lines.

4. Results

Fig. 3 shows δ^{15}N (in the upper part of each panel) and δ^{13}C (in the lower part) for dentin serial sections for the first molars of all six individuals. δ^{15}N and δ^{13}C are plotted on the vertical axis, while

Table 2
Size and attrition scores for each tooth in this study, and the number of isotopic serial samples ultimately analyzed.

Burial	Tooth	Attrition Stage	Root Tip - CEJ (mm)	CEJ-Occlusal Surface (mm)	Number of Samples*	C/N Ratio Range	Collagen Yield (%)
59	RM$_3$	3	14	4	9	3.1–3.2	9.3
59	RM$_2$	4	13	4	10	3.2–3.2	10.7
59	RM$_1$	5	12	3	10	3.2–3.3	11.6
79	LM$_1$	6	12	5	9	3.3–3.4	10.3
87	LM$_1$	2	9.5	6.5	9	3.3–3.4	9.0
92	LM$_1$	7	12	4	5	3.6–4.4	0.9
107	LM$_1$	5	10	5	5	3.2–4.0	0.8
275	RM$_1$	5	12	6	7	3.4–3.5	8.7

Notes: * - This column reports the number of isotopic samples actually run. All teeth were cut into 7–12 sections, but in some instances we had to combine collagen from adjacent apical sections to ensure enough collagen for reliable δ^{15}N and δ^{13}C isotope measurement. Attrition stage as reported in Wiberg (2010), and given according to system described in Smith (1984).

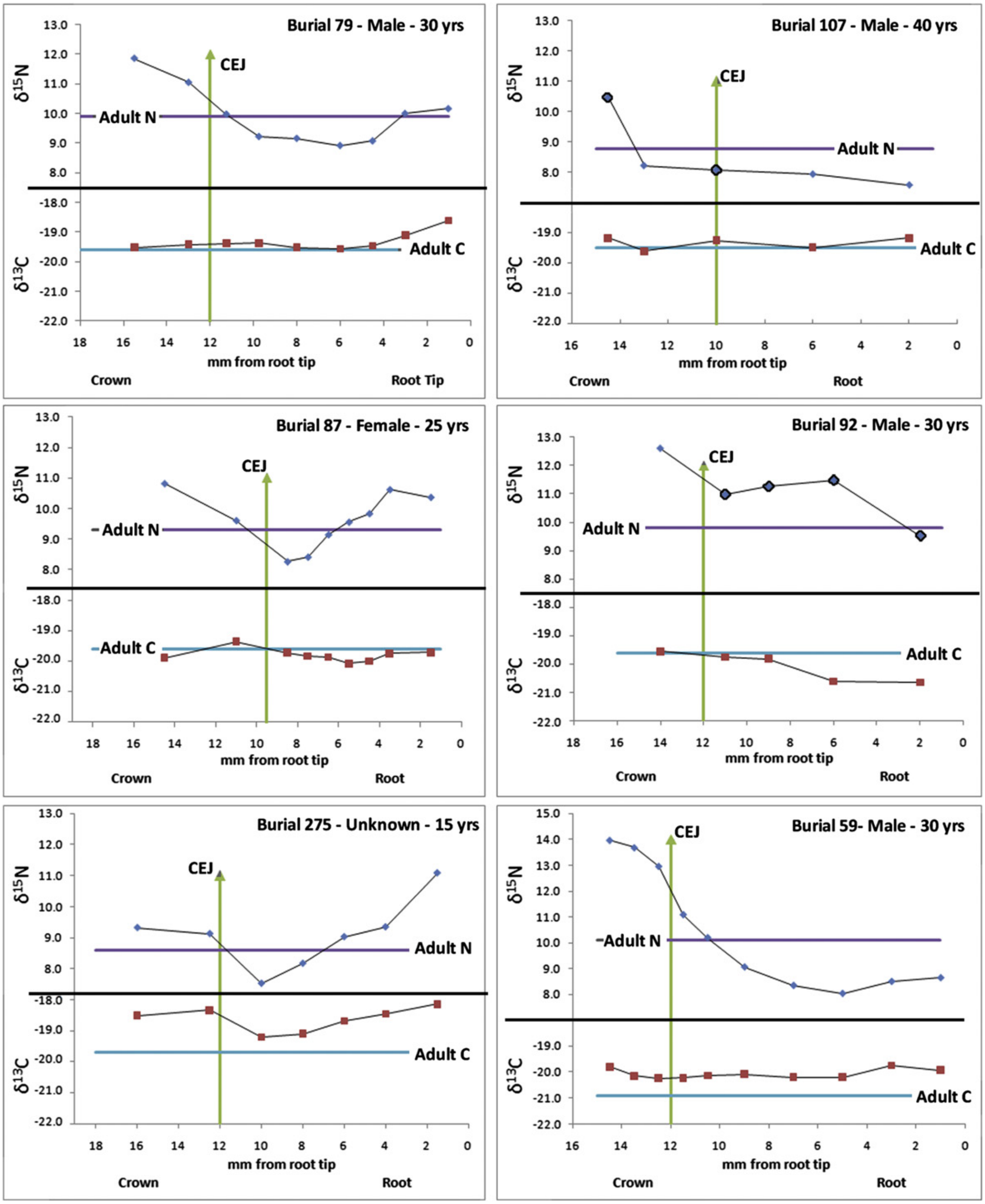

Fig. 3. Comparison of $\delta^{15}N$ and $\delta^{13}C$ in serial sections of six first molars.

distance from the apical root tip is plotted on the horizontal axis. Also shown, as horizontal bars, are the adult bone $\delta^{15}N$ and $\delta^{13}C$ to contextualize the dentin readings. The CEJ is also plotted as a vertical bar, representing a landmark on each tooth that facilitates comparison between teeth. Position on the horizontal axis represents the median value for a serial section. Thus, the isotopic values for a serial section taken between 8 and 10 mm from the root tip are plotted at 9 mm.

Fig. 3 shows that all six first molars follow a similar pattern. We assume that the adult bone collagen $\delta^{15}N$ represents an "adult food" signal, typical for what that individual consumed in adulthood. Within the serial samples, the $\delta^{15}N$ value begins high on the left, representing the earliest growth remaining on a tooth (ca. age 0–2 depending on attrition). The $\delta^{15}N$ value is typically 2–3‰ above the adult solid food diet at this point, and then steadily decreases in all subsequent serial samples. Most often, $\delta^{15}N$ values reach a minimum in samples at or just after the CEJ, although in one case (Burial 107) the $\delta^{15}N$ value decreases and then stabilizes well before the CEJ, and in another instance (Burial 92), it decreases well after the CEJ closer to the time when the apex of the root formed.

Together, we interpret the decreasing $\delta^{15}N$ pattern as a weaning signal, indicating a drop in trophic level from the mother's breastmilk early in the sequence to complementary solid or liquid foods in the middle and end. A 2–3‰ drop is consistent with what would be expected for a single trophic level decrease (Minagawa and Wada, 1984; Schoeninger, 1985). The data from Fig. 3 indicate that there is considerable variation in the weaning process, in both the rate of decreasing breastmilk consumption, the age of completion, and the composition of early childhood diets.

Collectively, all six first molar samples show $\delta^{15}N$ decreases from 14 to 10‰ to around 7–9‰. Except in Burial 92 (the tooth with problematical C:N ratios), $\delta^{15}N$ dips well below that of the adult diet, typically by 1–2‰. This pattern indicates that the majority of post-weaning protein was from a low trophic level source, likely C_3 terrestrial vegetal foodstuffs. One likely scenario for this population is the introduction of increasing amounts of acorn gruel as a substitute for breastmilk. Indeed, paleobotanical analyses show that burnt acorn nutshell is common at CCO-548 (Stevens et al., 2009; Wiberg, 2010). Schurr (1997) observed a similar effect at the Angel Site in the lower Ohio Valley, where children aged between 5 and 15 typically had about 0.6‰ lower $\delta^{15}N$ in bone collagen than adults. He was unsure whether this difference reflected real dietary differences between adolescents and adults, where children were eating a higher proportion of plant foods, or differences in nitrogen metabolism, for example, due to greater amino acid synthesis in children.

Two of the burials, 87 and 275, show an unexpected post-weaning trend, where $\delta^{15}N$ increases markedly, well above the adult solid food signal. The $\delta^{15}N$ values reach or exceed the pre-weaning levels to around 11‰. This pattern indicates consumption of relatively high trophic level foods during the childhood years for these two individuals. We consider the implications of this result below.

Relative to $\delta^{15}N$, $\delta^{13}C$ isotope ratios are much more stable within the dentin serial sections. The highly negative $\delta^{13}C$ values indicate that marine and/or C4 plant foods were not a significant part of the weaning diet. Four of the six individuals (Burials 59, 92, 107 and 275) show positive covariation between $\delta^{13}C$ and $\delta^{15}N$ in the early serial sections, that is, sections formed prior to full weaning. In these sections, $\delta^{13}C$ and $\delta^{15}N$ decrease in concert. However, in two cases (Burials 79 and 87) there is a slight negative covariation between $\delta^{13}C$ and $\delta^{15}N$ in the early-growing sections, indicating no association. We consider these results in greater detail below. In the post-weaning sections, $\delta^{13}C$ and $\delta^{15}N$ covary strongly in two individuals (Burials 79 and 275), weakly in two others (Burials 87 and 59), and not at all in a third (Burial 107). Burial 92 does not appear to have serial sections that post-date weaning. We interpret this positive covariation as the incorporation of modest amounts of marine-derived protein (e.g., salmon, shellfish) in the early childhood diet. Marine-based foods often have high $\delta^{15}N$ because there are more trophic levels in the food chain, and are also relatively heavy in ^{13}C. As a result, when marine foods are being consumed, there should be some positive correlation and covariation between $\delta^{13}C$ and $\delta^{15}N$ values.

Finally, for one individual, Burial 59, we also sampled a second and third molar in a similar fashion (all from the right side of the mandible). We wanted to verify that isotopic patterns were different in these teeth than the first molar. Such a finding would support our contention that shifts in $\delta^{15}N$ and $\delta^{13}C$ in the first molar do indeed represent weaning and not some phenomenon of tooth formation in general. As well, because the growth of dentin in the three molar teeth overlaps in time, this sampling strategy allowed us to examine dietary patterns up to ages 20–22 years, when the root of the third molar is complete. Fig. 4 shows the $\delta^{15}N$ chronological sequence represented by the three molar teeth.

As seen in Fig. 4, $\delta^{15}N$ patterns in the second and third molars are quite unlike the first molar. There is comparatively little variation in $\delta^{15}N$, especially in the third molar. This suggests that the trophic level of dietary protein stabilized after about age 10 for this individual, shortly after the roots of the second molar start forming. By contrast, there is much greater variation in $\delta^{13}C$ in the second and third molars relative to the first molar. Because C_4 plant food sources are rare in Central California, it appears that fluctuations in marine-derived protein were low in the first 6 years, but higher thereafter, especially between ages 12 and 22. It is possible that such a trend records increasing mobility on the part of this male, perhaps to and from locations to the east of CCO-548 where marine protein would have been unavailable.

5. Discussion

Although our sampling strategy increases the individual-scale resolution of dietary changes, there are still some issues of resolution because our serial samples are not mutually exclusive in the

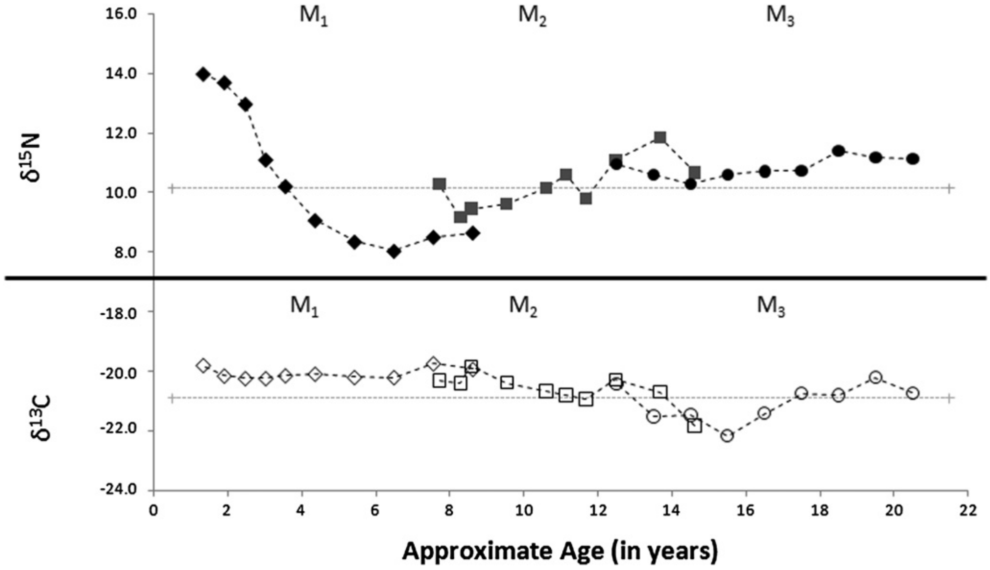

Fig. 4. Serial sections of the first, second, and third molar from one individual, showing dietary patterns over the first 20–22 years.

time and growth they represent. Sections overlap with preceding and subsequent sections. In the crown, this problem is minimized because dentin growth lines are nearly horizontal. In the root, however, growth lines are oriented at an oblique angle relative to the pulp cavity (as depicted in Fig. 2). In three dimensions, these growth lines form as cones with truncated tops. We were unable to cut the teeth using a scalpel along the growth lines. We note, however, that in most cases alternating samples (e.g., B and D, or C and E in Fig. 2) contain little or no dentin in common and are mutually exclusive or nearly so.

First molars begin growing at birth at the DEJ. As mentioned, this landmark is usually absent in our samples. The crown in a first molar completes growing between the ages of 2.5 and 3 (Hillson, 1996: 123; Liversidge et al., 1993:311). We calculated the midpoint, and assigned 2.75 years of age at the CEJ. Using an average dentin crown height of 4.8 mm (i.e., the DEJ-CEJ distance; calculated from individuals at CCO-548), we calculated a rate of growth of 1.75 mm per year in our sample for dentin in the crown, and used this figure to calibrate our age estimates. By contrast, root tips of first molars complete growth between the ages of 8 and 11 years, and we assign the value of 9.5 years to this landmark, or 6.75 years after the CEJ forms (Dean, 2009; Hillson, 1996: 123). The average length of roots (i.e., the CEJ-root tip distance) for a sample of M1 teeth from CCO-548 is 12.6 mm. We assume a linear rate of growth between the CEJ and root tip, and calculate a rate of 1.87 mm per year. We realize that actual rates vary between individuals (e.g., Dean et al., 1993; Dean and Vesey, 2008; Liversidge et al., 1993). As well, Dean (2009) shows that growth rates vary slightly within a tooth, with most rapid growth around ages 4–6 and tapering off during the final 2–3 years of growth. This information is used to calibrate time within the tooth to calculate the onset and completion of weaning in approximate years, shown in Table 3.

As mentioned, our samples time-average growth, especially within the root where dentin growth bands form as cones. Our sampling method is such that each of our serial sections incorporates dentin from the preceding and succeeding sections. In an effort to account for this effect, we examined photomicrographs of human first molars (Dean et al., 1993), noting the orientation of the growth lines in the dentin. Table 3 shows our estimate of the percentage of overlap between serial sections. The root is divided into 2 mm sections, while growth in the crown is divided into 1 mm sections, according to a typical sampling of a tooth in our methodology. The crown has a finer scale because, due to greater volume, we were often able to take more closely-spaced serial sections and still produce 1 mg of collagen. The rows in Table 3 correspond to growth increments during a certain time period, measured in years after birth (beginning and ending). The mm values for this growth correspond to the distance along the exterior surface of the tooth where this growth appears from the apical root tip. The columns indicate how much of that growth would appear in a horizontally-cut serial section according to our sampling strategy. For example, dentin that accrued between 1.7 and 2.3 years of age comprises 44% of the dentin in the serial section between 16 and 17 mm from the root tip, 17% of the dentin from the section between 15 and 16 mm, and 7% of the dentin of a section between 14 and 15 mm. Likewise, the serial section between 8 and 10 mm from the root tip comprises 30% dentin that formed between 4.4 and 5.5 years, 57% of dentin that formed between 5.5 and 6.6 years of age, and 13% dentin that accrued between 6.6 and 7.7 years of age.

Using the information in Table 3, we modeled four different weaning scenarios, and how they would appear had we sectioned that tooth using our sampling method. The models include a scenario where weaning happened abruptly (no weaning period) at the CEJ (2.75 years = 13 mm from tip), where weaning happened gradually across the CEJ over a period of approximately 2 years, where weaning is abrupt but early in life before the CEJ forms, and where weaning is abrupt but later in life after the CEJ forms. Fig. 5 shows the results of this modeling exercise.

Using these modeled curves, and comparison to the data for the six individuals shown in Fig. 2, we estimated the approximate age of weaning for each burial. We also estimated whether the weaning transition was abrupt (i.e., rapid) or gradual (i.e., slow) based on the rate at which δ^{15}N decreases. As well, when enough of the crown was present, we present a minimum length of time between the introduction of significant quantities (i.e., enough to shift isotopic values by more than 0.2‰) of complementary foods and the termination of breastfeeding. Finally, based on the post-weaning values of δ^{15}N, especially relative to the adult diet, we also estimate the composition of foods used to wean these individuals. As mentioned earlier, four individuals appear to have been weaned on a low trophic level resource, almost certainly a C_3-vegetal source such as acorn gruel. However, terrestrial herbivore or freshwater fish protein may have also contributed as weaning foods for some individuals. Table 4 shows these estimates.

Our age of weaning estimates for the six individuals from CA-CCO-548 are within the range reported for other hunting and gathering groups (Barry and Paxson, 1971; Konner, 2005:57), although four individuals appear to have terminated the weaning process at a later age than the average of approximately 3 years reported for a number of hunter-gatherer societies (see Robson et al., 2006: 28, Table 2.1:22–23). Together, the six individuals suggest an average cessation of breastfeeding around 3.6 years of

Table 3

Percentage of growth overlap between serial sections. The root is divided into 2 mm serial sections and the crown into 1 mm serial sections. Serial sections (as we sampled) appear as columns, growth sections (as the tooth grew) appear as rows.

Serial Sec. (mm) Growth Sec. (mm)		Beg. Age (yrs)	End Age (yrs)	17–18	16–17	15–16	14–15	13–14	12–13	10–12	8–10	6–8	4–6	2–4	0–2
DEJ	17–18	0	0.57	23											
Crown	16–17	0.57	1.1	68	1										
	15–16	1.1	1.7	9	31	8									
	14–15	1.7	2.3		44	17	7								
	13–14	2.3	2.8		15	48	25	9							
Root	12–13	2.8	3.4			27	39	63	29						
	10–12	3.4	4.4				29	29	49	26					
	8–10	4.4	5.5						19	47	30				
	6–8	5.5	6.6						3	27	57	42			
	4–6	6.6	7.7								13	57	45		
	2–4	7.7	8.7									1	55	57	
Root tip	0–2	8.7	9.5											43	100

Notes: Sec. = Section; Beg. = Beginning Age of formation for this growth sect2ion. CEJ at 13 mm from apical root tip. DEJ at 18 mm from apical root tip. Columns sum to 100%.

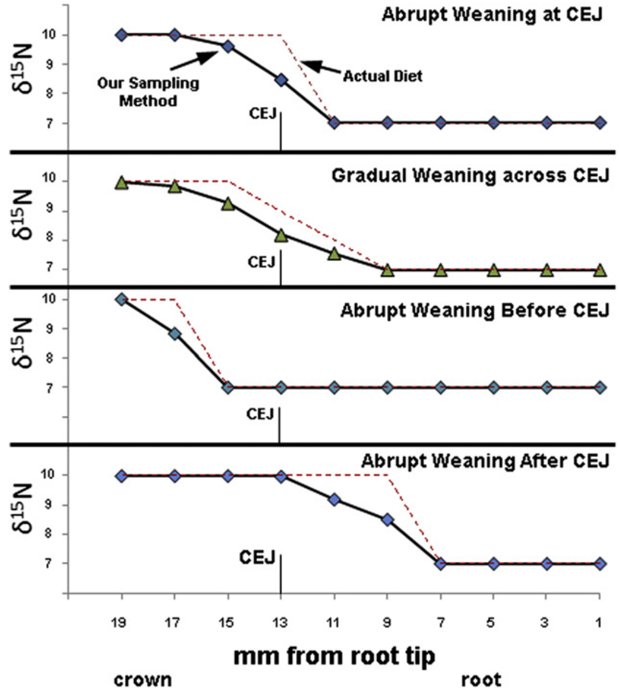

Fig. 5. Models of weaning and resulting sampling curves.

age (3.0 years if we remove Burial 92), and a minimum average of 1.1 years for the entire weaning process (Burial 92 excluded).

There is a great deal of variation in weaning behavior within our small sample of six. Some of this variation may be explained by changes in weaning practices over the 600-year time span represented in our samples. However, even in the four individuals (Burials 59, 79, 87, 275) that date closer in time (within a 200 year interval), there is high variation. Moreover, such a finding is also in line with studies among modern societies, where there is tremendous intra-population variation in weaning behaviors (Sellen, 2006; Stuart-Macadam and Dettwyler, 1995).

One individual, Burial 107, appears to have been weaned very early in life relative to the five other samples we analyzed, by about age 1. This individual was also unusual in that he was one of just a few individuals ($n = 17$ out of 480 total) buried with at least one charmstone. As well, he was just one of six individuals at the site buried with a trophy head. Clearly Burial 107 was unusual in status as an adult. Whether there is a correlation between his status as an adult and his early age of weaning is not known, but warrants additional research. Toward this end, we are now examining weaning for other individuals buried with charmstones and trophy heads from the site. The five other burials in this study had very few or no grave goods associated with them. By contrast, Burial 59 appears to have been weaned much later in life, after the age of 4, and Burial 92 appears to have been completely weaned even later. However, we treat Burial 92 with caution because we were only able to run five serial samples, minimizing the precision of our age-specific estimates, and four of the five serial samples had C/N values above 3.6. We hope that with additional research we can determine whether Burial 92 is truly an outlier, suggesting, perhaps, that poor collagen preservation may explain the unusual age estimate, or whether very late weaning was occasionally practiced at CCO-548.

Table 4
Final estimates of age of weaning, including completion of the weaning process, the rate of weaning, the minimum length of time for the weaning process, and the general source of weaning foods.

Burial #	Completion of Weaning (yrs)	Rate of Weaning	Minimum Length for Weaning Process (yrs)**	Weaning Food
59	4.2–5.2	Gradual	2–3	Adult-like
79	3.2–3.9	Intermediate	n/a	Low-trophic
87	1.9–3.3	Abrupt	0–1.4	Low-trophic
92*	5.8–7.7	Gradual	n/a	Adult-like
107	1.0	Abrupt	0–1	Low-trophic
275	2.4–3.8	Abrupt	0–1.4	Low-trophic
Average	3.1–4.1		0.5–1.7	

Notes: * - Data for Burial 92 should be treated with extra caution, given poor state of collagen preservation. ** - The length of the weaning process represents a minimum amount of time between the introduction of significant amounts of non-breastmilk protein and the termination of breastmilk.

As mentioned, Burials 87 and 275 display an unusual increase in δ^{15}N shortly after weaning, indicating consumption of a significant amount of high trophic level resources during early childhood. For Burial 87, a female, this transition appears to begin around age 6.4 and for Burial 275, sex unknown, around age 6.1. This signature could represent high parental or societal investment in certain children during later childhood years. For example, adults may have provisioned these individuals with greater quantities of high-quality and protein-rich foods, such as hunted game or fish. It is also possible that these individuals moved residence during their early childhood years to a location where such foods were in greater supply, an intriguing possibility that could be tested by further isotopic analyses (e.g., Sr isotope ratios).

A third intriguing possibility is that such a signal may not represent foods provided by others, but instead represents an early childhood foraging strategy that focused on resources available near CCO-548. Early childhood foraging among hunter-gatherers has received increasing interest among anthropologists in recent years (e.g., Bird and Bliege Bird, 2005; Blurton Jones et al., 1994, 1997; Sugiyama and Chacon, 2005). For example, studies among the Martu of the Australian Western Desert suggest that in pre-contact times, children would often hunt medium-sized lizards and small birds and would gather grubs, bird eggs or bulbs (Bird and Bliege Bird, 2005:135). Likewise, children among the Hadza spend considerable time foraging for roots and berries and can achieve return rates between 50 and 70% of adults (Hawkes et al., 1995, and in a multiethnic community in Botswana, children were effective at fishing and collecting mongongo nuts (Bock, 2005). In most cases, a large portion of the food collected by children was consumed by them as well. The same is not apparently true for !Kung children, who do very little foraging by comparison (Hawkes et al., 1995). If the individuals represented by Burials 87 and 275 were gathering their own food around CCO-548, they were clearly focusing on foods from a higher trophic level than they typically consumed as adults. It is not yet possible to pinpoint the species represented by such a diet, but on the edge of the California Delta, such foods may have included freshwater fish, snakes, turtles, and/or a range of smaller insectivorous species such as lizards or frogs. Return rates for such species are typically low causing adults to pass them by. But for children who do not have the strength and experience to hunt and gather as efficiently as adults (see discussion in Bock, 2005), they may have comprised important complementary foods. Many of these remains are found among the faunal assemblage at the site (Stevens et al., 2009; Wiberg, 2010: 243). We hope to further explore these three possibilities with additional research at CCO-548.

While the δ^{15}N values seem to record a strong weaning signal, as we expected, the δ^{13}C values do not show as strong a pattern. In a previous study with modern human infant fingernail clippings, Fuller et al. (2006a) found, in addition to a 2–3‰ decrease in δ^{15}N, a 1‰ drop in $\delta^{13}C$ during weaning. In our study, four of the six individuals (including Burial 92 with poor C:N ratios) show a $\delta^{13}C$ drop that generally mirrors $\delta^{15}N$. The magnitude of the drop is slightly less than Fuller et al. observed, averaging only 0.7‰, but these results provide support for the findings of Fuller and colleagues. However, in two burials (79 and 87) this is not the case, where $\delta^{13}C$ tends to increase (79) or fluctuate (87) during weaning. Why $\delta^{13}C$ in these two individuals behaves differently is not clear. Fuller et al. (2006a) suggest that $\delta^{13}C$ may change more in accord with the introduction of complementary food, rather than the entire weaning process. Thus, one possibility is that, because many of our teeth were missing the earliest sections of dentin growth due to occlusal attrition, $\delta^{13}C$ may have decreased with weaning in these two individuals but we did not detect that signal due to loss of the earlier forming dentin. Such an explanation might explain Burial 79, which had a wear stage of 6 (heavily worn), but not Burial 87, which had a wear stage of only 2 (slightly worn). Additional research with a larger sample will be necessary to resolve this issue.

6. Conclusions

Improvements in the sensitivity of mass spectrometers now allow for the analysis of very small samples of collagen for stable nitrogen and carbon isotopes, while maintaining good instrument precision. Currently at the Stable Isotope Facility (SIF) at UC Davis, approximately 1 mg of collagen is needed per sample. This small sample size allows us to cut first molars into serial sections and extract collagen from each, permitting the examination of changes in diet over the first 9 years of life. The same principle holds for other teeth as well, as we have shown with a second and third molar from the same person. Importantly, this approach focuses on dietary patterns within individuals, rather than populations, and facilitates comparing weaning and diet among different segments of a population, such as males and females or individuals who died at different ages. This scale of analysis contributes to a range of ongoing anthropological debates regarding the evolution of humans and the timing of various life history events, such as the age of weaning and early childhood foraging strategies.

One obstacle to sectioning teeth involves the way in which they are cut. Currently, we are taking horizontal sections out of the dentin. Because growth occurs in concentric cones, our sections time-average changes in diet. An alternative means to take serial collagen samples would be a significant improvement to our methodology. Indeed, we anticipate that laser ablation systems coupled to light stable isotope ratio mass spectrometers will solve this issue in the future, and will facilitate even finer-grained analyses of dietary change.

A second arena where improvements are possible concerns using average values for first molar growth (e.g., the crown is complete at age 2.75 and the root at age 9.5) as a means to track time within an individual. Dean (2009) and others show that there is much variation between individuals. A method for tracking age within a tooth that is specific to that individual would significantly improve the precision of our estimates.

A third issue concerns the formation of secondary dentin in teeth. Secondary dentin is deposited within the pulp chamber and root canal during adult years (Hillson, 1996:194), and as such, will have a different isotopic signature than primary dentin. Secondary dentin was not easily visible to the naked eye in our sample, thus we were not able to identify and separate primary from secondary dentin. However, two lines of reasoning suggest the effects of secondary dentin in reconstructing age of weaning in our sample are minor. First, because the pulp chamber and especially the root canal are small relative to the total volume of the tooth, the mass of secondary dentin is expected to be minor compared to primary dentin in a serial section. Thus, the major signal in a serial section should be from primary dentin. Second, if secondary dentin forms throughout the pulp chamber and root canal, the effects will be averaged out across the serial sections of a tooth. Thus, although the absolute $\delta^{13}C$ and $\delta^{15}N$ may change, the relative differences across serial sections will not. Because we use the latter to estimate age of weaning, secondary dentin formation should not substantively interfere with our results. Indeed, secondary dentin should have an isotopic composition similar to that in adult bone. The fact that $\delta^{13}C$ and $\delta^{15}N$ values in the teeth rise above and fall below adult bone, suggests that the effects of secondary dentin are minor.

Methodological limitations aside, our analyses of six individuals who lived between 3700 and 3100 years ago from CCO-548 indicate an age of weaning within the range of other studied modern hunter-gatherers. The weaning process often lasted several years and was generally complete by the end of the fourth year of life. However, the data show significant differences between individuals. Some individuals were weaned abruptly, with the process lasting less than one year, while for other it appears to have been at least three years. Likewise, using median values and ignoring burial 92 that had more marginal collagen preservation, the cessation of breastmilk varied between 1 (Burial 107) and 4.7 (Burial 59) years of age. The source of the weaning food in most cases appears to have been a low trophic level food, likely a vegetable-based product such as acorn mush. Intriguingly, the one individual in our sample (Burial 107) who was buried with unusual grave goods was also a clear outlier in terms of the age of weaning, having been completely weaned on or before his first year of life.

Our analyses also showed interesting differences between individuals in early childhood diet, after weaning was complete. Two of the six burials suggest consumption of higher trophic level foods shortly after being weaned, much higher than what they consumed as adults. What those foods may have been is not known, but may imply a Hadza-like foraging strategy, where these individuals were gathering a significant portion of their own diets as children. On the edge of the California Delta marshlands, such resources could have included animals that inhabit the nearby wetlands and consume other animals (e.g., fish, snakes, turtles, etc.). Alternatively, such patterns could indicate translocation early in life or an alternative pattern of provisioning for children by adults in the community.

Clearly, there is still much to be learned about dietary patterns early in life in ancient populations. Our methodology shows how we can unlock that information with a micro-sampling approach. As well, we can make a greater contribution to telling the stories and life histories of particular individuals from the past, as well as to large-scale debates about the evolution of human societies.

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