Establishment of a Greek Food Database for Palaeodiet Reconstruction: Case Study of Human and Fauna Remains from Neolithic to Late Bronze Age from Greece

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Abstract: We review the stable isotopic data of recovered Greek bones from the Early Neolithic to the Late Bronze period in order to examine dietary changes over time. As an isotopic baseline we use the published fauna data of the periods. The analysis revealed a diet that included a significant proportion of foods based on C3 plants, and the bulk of the animal protein must have been provided by terrestrial mammals with a small but detectable proportion of marine protein for coastal and island populations. A more significant contribution of marine protein is observed for Bronze Age populations while the enrichment in both C and N isotopes is connected, for some areas, to the introduction of millet during the Bronze Age, and to freshwater consumption. An extensive database of Greek food sources is presented and compared to the fauna from the prehistoric periods (Early Neolithic to Late Bronze Age) of the literature. We propose that this database can be used in palaeodiet reconstruction studies.

Keywords: stable isotopes; palaeodiet; carbon; nitrogen; bone collagen; Bronze Age; Neolithic; Ancient Greece

1. Introduction

Stable isotopic analysis has been used to reconstruct the diet of past populations. The stable isotopic values $^{13}$C and $^{15}$N are used: to identify the introduction and spread of maize agriculture in the Americas [1] and millet cultivation in eastern Europe [2]; to distinguish between marine and terrestrial nutrients in the diet [3–7]; to recognize the proportion of legumes vs. non-legumes alimentation [8]; to distinguish between nitrogen-fixing and non-fixing plants; to examine dietary differences between contemporaneous populations [9]; to determine dietary differences (e.g. age, sex, and status differences) within populations [10–15]; to investigate infant feeding practices [16–18], and to observe dietary changes over time [19–21].
Although human remains are abundant, especially in Greece where there are numerous Holocene archaeological sites, very little is known regarding where and how people lived and what constituted their diet and habits.

The objective of this study is to reconstruct the diet of the populations living in Greece from the Early Neolithic to the Late Bronze period in order to examine a) the relative contribution of marine vs. terrestrial nutriments in the diet and b) explore possible chronological variations in the diet. To achieve the objectives of this study, we review published stable isotopic results of Greek human bones from the Early Neolithic to the Late Bronze period in relation to fauna data of the same periods as food sources. Measurements of $^{15}$N and $^{13}$C in recent Greek human samples (hair) and measurements of contemporary Greek food sources are also presented. These contemporary food sources are compared with the available fauna data of the studied periods in order to examine if they can be used as baseline indicators. This is especially important for marine food sources, where very few samples from the above periods are available.

1.1. Background on Stable Isotopes

The collagen of fossil bone and dentine should preserve C and N isotopic signatures, reflecting the dietary preferences of the individual. In particular, a stable carbon and nitrogen isotope ratio of bone and tooth collagen provides direct evidence of diet, and reflects the average isotopic composition of an individual’s intake of dietary protein as well as other nutrients [7,8,22] over a period of 10 years or more [23].

The stable carbon isotope analysis of collagen has been an effective tool for reconstructing the vegetable dietary patterns since the plants that follow different photosynthetic pathways exhibit different $\delta^{13}$C values. The C3 plants (temperate region plants, some subtropical grasses, including wheat, rice, barley, all trees, shrubs, nuts and fruits) have $\delta^{13}$C values ranging from $-20‰$ to $-35‰$ [24]. Due to fractionation, the $\delta^{13}$C value of the consumer’s bones collagen is approximately $5‰$ higher than that of their diet, and populations that consume only C3 plants have $\delta^{13}$C values from $-20‰$ to $-21‰$ [3,5]. The C4 plants (tropical grasses, maize, sugar cane, millet, sorghum, some amarants and some chenopods) have $\delta^{13}$C values between $-34‰$ to $-14‰$ [24] and populations with diet rich in C4 plants have $\delta^{13}$C values as high as $-10‰$ [27]. Furthermore, the isotopic composition of bone collagen is mainly controlled by protein consumption, while the bone apatite reflects the whole carbon isotope ratios. A combination of collagen and apatite $^{13}$C measurements may introduce additional information [22] for the reconstruction of dietary habits, especially in mixed diets, as the consumption of fat from large marine animals and the consumption of carbohydrates from underground plants [26,28,29]. The isotopic preservation of bone apatite remains a serious concern but careful screening of the bone samples for alteration should reveal situations where bones retain useful information [30]. Another possible factor that must be considered when analyzing the isotopic values of $^{13}$C and $^{15}$N of bone collagen is the case when dietary protein is insufficient for tissue building and collagen amino acids might partially originate from other sources, such as carbohydrates [31,32]. That might be the case in regions of the Mediterranean where the reported high human $\delta^{15}$N values indicate consumption of marine foods, yet the low $\delta^{13}$C values indicate a terrestrial diet [31–34]. A possible explanation is that while nitrogen from marine foods was adequate for amino acid synthesis, marine carbon was insufficient to synthesize all the necessary amino acids in collagen, causing $\delta^{13}$C to be supplied from low $^{13}$C terrestrial sources (lipids and carbohydrates) [29].

Dietary reconstruction using stable nitrogen isotope analysis of bone collagen reproduces the trophic level, or the position of an individual in the food chain. So, the $\delta^{15}$N values of herbivores are approximately $3‰$ higher than the plants they consume [4,35] while carnivores have $\delta^{15}$N values that are approximately $3‰$ higher than the herbivores that they consume [4,35].

Carbon and nitrogen isotope ratios can also be used to investigate the proportion of terrestrial and marine nutriments in environments since marine animals and fish are systematically enriched by about $7‰$ with respect to terrestrial consumers [5]. Most marine carnivores (fish, seals) have
\( \delta^{15}N \) values greater than 12\( \%_o \), while terrestrial plants and animals have values ranging from 0\( \%_o \) to 10\( \%_o \) [36]. Freshwater animals have more positive \( \delta^{15}N \) values than their terrestrial counterparts, whereas their \( \delta^{13}C \) values are relatively similar, and freshwater resources present in small rivers are readily distinguishable from fully terrestrial resources [12]. The \( \delta^{15}N \) value of human bone collagen is consequently about 3\( \%_o \) higher than the \( \delta^{15}N \) value of the protein that the human has consumed [4,35,37]. Humans who obtain the majority of their dietary protein from marine species have \( \delta^{15}N \) values ranging from about 12\( \%_o \) to 22\( \%_o \) [38,39] while those who consume only terrestrial protein sources have \( \delta^{15}N \) between 5\( \%_o \) and 12\( \%_o \) [39].

In coastal areas where populations may have been consuming both marine resources and C4 plants [20,40], stable nitrogen and carbon isotope analysis is fundamental in order to distinguish between dietary proteins derived from marine resources vs. terrestrial foods [38]. Stable nitrogen isotope analysis can also be used to identify vegetable vs. non–vegetable eating, as vegetables have lower \( \delta^{15}N \) approaching 0\( \%_o \). Climate may also affect the \( \delta^{13}C \) and \( \delta^{15}N \) values of terrestrial animals through its effect on the \( \delta^{13}C \) of plants [41,42] and on the \( \delta^{15}N \) of soil [43–45], at the base of the food chain.

1.2. Background on Ancient Greek Diet

Dietary habitudes of the Greek population were based on palaeobotanical and zooarchaeological analyses. Palaeobotanical study has been conducted to examine legume consumption [46] and the identification of plant phytoliths in order to distinguish between olive oil and wine [47]. In contrast zooarchaeological studies indicate that sheep and goats were the main source of meat in the Mediterranean region [48].

An indirect but important source of information on the diet of the ancient Greeks is the archaeological evidence such as plant remains, animal bones, food preparation utensils, and storage vessels. Food and drink offerings are also another source of information on the diet of the ancient Greeks. In the Neolithic period, the main source of nutrition was cereals, most notably wheat, fresh fruits, nuts and meat [18]. This is presumed to be so, because this period is characterized by the appearance of organized agricultural groups and the beginning of the domestication of plants and animals. The selection of food in the Neolithic settlements is connected to factors such as climate, geographical location, the cultural background and the local resources and landscape. So, it is assumed that Greek Neolithic populations’ diet was primarily terrestrial, based on C3 plants (wheat, barley, legumes). Meat and dairy products (from domestic animals) as well as wild resources (ex. Cervus elaphus, Sus scrofa, [49–52]) were, also incorporated into the diet, but to a lesser extent. This in accordance with the zooarchaeological observations, which also indicate that livestock was subsidiary to crop growing [53,54]. Furthermore, only occasional or periodic exploitation of near-shore marine or freshwater protein resources is assumed.

During the Bronze period the diet became more variable with the introduction of more cereal crops, wheat, barley and millet that constituted the primary source of protein. Also in this period vegetables, fish and meat are becoming more easily available and milk, wine, olive, are introduced in their alimentation [18]. The main source of meat in the Mediterranean region was sheep and goats although it is unknown to what extent these animals were also used for their milk. Meat was considered a luxury and was eaten only infrequently. Wild and domesticated birds were consumed only occasionally [55] although eggs may have been more commonly consumed. Fish were eaten less frequently than other foods [56]. According to literary sources significant dietary differences between the upper and lower classes and between males and females existed among the Greeks [57].

In Table 1 we present the key conclusions on the diet for all the sites according to the bibliography.
Table 1. Key conclusions for the sites reviewed and relevant bibliography (E. Neolithic: Early Neolithic, L. Neolithic: Late Neolithic, EBA: Early Bronze Age, MBA: Middle Bronze Age, LBA: Late Bronze Age).

| Site           | Period | Key Bibliographic Conclusions                                                                 | Bibliography |
|----------------|--------|-----------------------------------------------------------------------------------------------|--------------|
| Theopetra      | E.Neolithic | Primarily a C3 terrestrial diet. Very little of the dietary protein had a marine origin       | [58]         |
| Fragthi        | E.Neolithic | Primarily a C3 terrestrial diet. More significant amounts of meat and dairy products, and possibly marine foods. | [58]         |
| Alepotrypa     | L.Neolithic | Poor diet based mainly on C3 terrestrial resources with insignificant consumption of marine resources | [58,59]      |
| Kouveleiki     | L.Neolithic | Primarily a C3 terrestrial diet. Very little of the dietary protein had a marine origin       | [58]         |
| Tharrounia     | L.Neolithic | Terrestrial C3 plants and some consumption of animal protein (i.e. meat and/or milk produce). | [60]         |
| Kefalas        | L.Neolithic | Primarily a C3 terrestrial diet. More significant amounts of meat and dairy products, and possibly marine foods. | [58]         |
| Manika         | EBA     | C3 and few fish, consuming animal products (meat and/or milk) in high amounts                | [60,61]      |
| Perachora      | EBA     | Mix of terrestrial and marine resources, partial C4                                           | [61,62]      |
| Asine          | MBA     | C3 (meat, milk, dairy products)                                                              | [63]         |
| Argos          | MBA     | Homogenous C3 terrestrial diet                                                                | [50,61]      |
| Koufovouno     | MBA     | C3 resource consumption, ranging from wheat and legumes to dairy products and meat.          | [61,64]      |
| Korinos        | LBA     | Homogenous C3 terrestrial diet                                                                | [49]         |
| Rymnio         | LBA     | Homogenous C3 terrestrial diet                                                                | [49]         |
| Spathes        | LBA     | Homogenous C3 terrestrial diet                                                                | [49]         |
| Pineiada       | LBA     | Partial C4, C3 (meat, milk, dairy products)                                                   | [61]         |
| Voudeni        | LBA     | C3 plants and or animals and milk. No significant consumption of marine source                | [17,61,65,66]|
| Kalapodi       | LBA     | C3 (meat, milk, dairy products)                                                               | [17,61]      |
| Zeli           | LBA     | C3 (meat, milk, dairy products)                                                               | [17,61]      |
| Ag. Triada     | LBA     | Partial C4, C3 (meat, milk, dairy products)                                                   | [17,61]      |
| Kritika        | LBA     | C3 (meat, milk, dairy products)                                                               | [61]         |
| Almyri         | LBA     | Partial C4, C3 (meat, milk, dairy products)                                                   | [17,61]      |
| Trianta        | LBA     | C3 (meat, milk, dairy products)                                                               | [61]         |

2. Materials

A total of 363 human bone samples from 22 archaeological sites across Greece were examined in this study obtained from the literature [17,49–51,58–67]. Figure 1 shows the spatial distribution of the sites and the number of samples for each one of them (solid circles). Apart from the human bones, some data on faunal samples were also available from the same literature sources and are indicated in Figure 1 (open circles).

Analysis of 23 hairs samples (δ¹³C and δ¹⁵N) from the recent Greek population were conducted in the Stable Isotope Unit of NCSR “Demokritos”, Greece (Table 2). These hair samples are from a selected population (elderly people of both genders, having not traveled for at least five years prior to the sampling, constantly consuming local products as diet source and drinking only tap water).

Collagen samples from herbivore (n = 54), carnivore (n = 8), and flesh samples from marine low trophic level (n = 10), marine high trophic level (n = 22), freshwater fish (n = 8), birds (n = 5) and plant
samples of C3 (n = 124) and C4 (n = 13), were studied isotopically ($\delta^{13}C$ and $\delta^{15}N$) from Greek sources in the Stable Isotope Unit of NCSR “Demokritos” (Tables 3 and 4). The classification of marine samples to low/high trophic level was conducted according to Stergiou and Karpouzi (2002) [68].

3. Methods

For the contemporary Greek human samples, hairs were clipped from each subject, rinsed twice in distilled water for about 20 min each time. These samples were then dried overnight at 65 °C and ground to a fine powder (to be homogenized) before analysis.

The contemporary plant samples (C3 (n = 124) and C4 (n = 13)) were ground to a fine homogeneous powder (<250 µm size) under liquid nitrogen.

The contemporary fauna samples (marine low trophic level (n = 10), marine high trophic level (n = 2), freshwater fish (n = 8) and birds (n = 5)) muscle tissue was taken from each specimen and immediately frozen.

For the Herbivore (n = 54) and Carnivore (n = 8) samples, extraction of collagen from bone was based on those of Ambrose (1990) [69], which can be summarized as follows (see also Tykot...
Solid bone samples were first placed in 0.1 M NaOH to remove contaminants, followed by demineralization with 2% HCl, a second treatment with 0.1 M NaOH, and finally a 2:1:0.8 defatting mixture of CH₃OH, CHCl₃, and water. The dried and weighed samples were then analyzed with a FlashEA/IRMS for δ¹³C and δ¹⁵N.

The isotopic ratios \( \delta = (R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}} \times 1000 \) were measured versus atmospheric N₂ (AIR) and PDB (a marine carbonate) for nitrogen and carbon respectively. The reported values are the means of two or more consistent measurements of each sample. The standard deviation of the measurements ranges on average between ±0.1 and ±0.2‰ (2σ), for both ¹⁵N and ¹³C isotopes.

Collagen yields over 1 wt% are considered acceptable for carbon and nitrogen values [71], while the C:N ratio should range between 2.9 and 3.6 [72]. All our collagen samples were within these ranges as indicated in Table 2.

In order to compare contemporary ¹³C values of herbivores, carnivores and humans with the literature values of the Neolithic to Late Bronze age we applied a Suess effect correction [73] (we subtracted 1.5‰ from the values of Table 2 and Figure 2e). The Suess effect refers to the change in the ratios of carbon isotopes ¹³C:¹²C caused by the release of carbon (in the form of CO₂) from the burning of fossil fuels (burning fuels produces carbon dioxide, whose carbon consists almost entirely of the ¹²C isotope, and thus dilutes the ratios in all carbon reservoirs) and from land clearing (anthropogenic activities).

In order to compare the contemporary marine flesh samples with the ancient fish bone samples of the studied periods a mean fractionation value (4‰) [26] was added to the flesh ¹³C values of Table 3 to reflect the expected bone values.

In order to compare the contemporary human hair samples with the human bone samples of the studied periods a fractionation to ¹³C and ¹⁵N equal to 1.41‰ and 0.86‰ was added to the hair isotopic values respectively [74], to reflect the expected bone values.

In this study, we considered four diet sources, i.e., marine high, marine low, terrestrial plants and terrestrial animals and two stable isotope systems (δ¹³C and δ¹⁵N).

### 4. Results and Discussion

In Table 2 we present the isotopic ratios (δ¹³C and δ¹⁵N) of contemporary Greek humans (hair samples). In Table 3 we present the isotopic ratios (δ¹³C and δ¹⁵N) of contemporary animals from Greece (bones samples for the terrestrial animals and flesh samples for the marine animals). In Table 4 we present the isotopic ratios (δ¹³C and δ¹⁵N) of Greek plants (C3 and C4).

| Gender | Location          | Coordinates | δ¹³C | δ¹⁵N |
|--------|-------------------|-------------|------|------|
| male   | Naxos-Damarionas  | 37.05, 25.47 | −21.0 | 9.0  |
| male   | Naxos-Damarionas  | 37.05, 25.47 | −20.4 | 8.5  |
| female | Naxos-Damarionas  | 37.05, 25.47 | −21.1 | 9.3  |
| female | Imathia-Alexandria| 40.62, 22.44 | −20.1 | 9.3  |
| male   | Imathia-Alexandria| 40.62, 22.44 | −20.5 | 8.6  |
| male   | Corinthia-Manna   | 37.98, 22.51 | −21.2 | 7.6  |
| female | Corinthia-Manna   | 37.98, 22.51 | −21.9 | 7.6  |
| male   | Corinthia-Kamari  | 38.09, 22.57 | −21.1 | 8.8  |
| male   | Arta              | 39.15, 20.98 | −21.6 | 9.0  |
| female | Xios              | 38.38, 26.04 | −20.1 | 9.5  |
Table 2. Cont.

| Gender | Location          | Coordinates | $\delta^{13}$C | $\delta^{15}$N |
|--------|-------------------|-------------|----------------|----------------|
| female | Amfilochia-Stanos | 38.80, 21.17| −20.1         | 8.9            |
| female | Messenia-Kopanaki | 37.28, 21.81| −21.7         | 8.4            |
| male   | Messenia-Kopanaki | 37.28, 21.81| −22.0         | 7.8            |
| female | Messenia-Kopanaki | 37.28, 21.81| −21.7         | 7.7            |
| female | Messenia-Manesis  | 37.08, 21.89| −20.7         | 8.0            |
| female | Messenia-Avramiou | 37.67, 21.46| −20.5         | 8.4            |
| female | Halkidiki-Polygyros| 40.37, 23.44| −20.2         | 8.7            |
| male   | Halkidiki-Polygyros| 40.37, 23.44| −20.8         | 8.9            |
| female | Aetolia-Acarnania Chrisovitsa | 38.57, 21.70| −21.8         | 8.1            |
| male   | Kavala-Mirtofito  | 40.82, 24.19| −21.3         | 8.2            |
| female | Attiki-Athens     | 37.98, 23.73| −21.2         | 9.3            |

Table 3. Isotopic values of terrestrial and marine animals from Greece.

| Herbivore               | $\delta^{13}$C | $\delta^{15}$N | Location     | Lat.  | Lon.  | C/N | Collagen Yield (mg/g) |
|-------------------------|----------------|----------------|--------------|-------|-------|-----|------------------------|
| Sheep, Ovis aries       | −20.9          | 5.2            | Domestic     | 39.37 | 21.93 | 3.00| 190                    |
| Sheep, Ovis aries       | −20.1          | 5.8            | Domestic     | 35.34 | 25.14 | 3.12| 191                    |
| Sheep, Ovis aries       | −20.9          | 5.3            | Domestic     | 35.34 | 25.14 | 3.19| 187                    |
| Sheep, Ovis aries       | −21.3          | 5.1            | Domestic     | 35.34 | 25.14 | 3.17| 192                    |
| Sheep, Ovis aries       | −20.7          | 4.1            | Domestic     | 40.18 | 21.47 | 3.15| 189                    |
| Sheep, Ovis aries       | −20.6          | 6.3            | Domestic     | 39.37 | 21.93 | 3.20| 190                    |
| Sheep, Ovis aries       | −20.7          | 6.4            | Domestic     | 39.37 | 21.93 | 2.97| 188                    |
| Sheep, Ovis aries       | −20.4          | 6.3            | Domestic     | 39.37 | 21.93 | 3.11| 189                    |
| Sheep, Ovis aries       | −20.6          | 6.2            | Domestic     | 35.34 | 25.14 | 3.15| 191                    |
| Sheep, Ovis aries       | −20.6          | 6.3            | Domestic     | 35.34 | 25.14 | 3.21| 192                    |
| Sheep, Ovis aries       | −20.3          | 6.3            | Domestic     | 35.34 | 25.14 | 3.19| 190                    |
| Sheep, Ovis aries       | −20.4          | 6.4            | Domestic     | 35.34 | 25.14 | 2.99| 187                    |
| Sheep, Ovis aries       | −23.6          | 4.1            | Domestic     | 37.08 | 22.43 | 3.00| 189                    |
| Sheep, Ovis aries       | −24.0          | 4.5            | Domestic     | 37.08 | 22.43 | 3.13| 186                    |
| Sheep, Ovis aries       | −23.9          | 5.1            | Domestic     | 37.08 | 22.43 | 3.08| 191                    |
| Sheep, Ovis aries       | −22.8          | 5.1            | Domestic     | 37.08 | 22.43 | 3.09| 188                    |
| Sheep, Ovis aries       | −23.3          | 4.7            | Domestic     | 37.08 | 22.43 | 3.14| 191                    |
| Sheep, Ovis aries       | −21.3          | 6.4            | Domestic     | 40.51 | 23.63 | 3.18| 189                    |
| Sheep, Ovis aries       | −21.5          | 5.6            | Domestic     | 40.51 | 23.63 | 3.04| 190                    |
| Tortoise, Testudinidae  | −23.4          | 6.1            | Wild         | 40.18 | 21.47 | 3.19| 189                    |
| Hare, Lepus sp.         | −21.8          | 5.8            | Wild         | 39.37 | 21.93 | 3.21| 181                    |
| Rabbit, Oryctolagus cuniculus | −23.5      | 3.9            | Domestic     | 39.37 | 21.93 | 3.15| 179                    |
| Wild boar, Sus scrofa   | −19.9          | 4.9            | Wild         | 39.37 | 21.93 | 3.21| 220                    |
| Wild boar, Sus scrofa   | −19.4          | 5.1            | Wild         | 39.37 | 21.93 | 3.15| 222                    |
| Wild boar, Sus scrofa   | −19.6          | 5.3            | Wild         | 39.37 | 21.93 | 3.02| 224                    |
| Pig, Sus scrofa domesticus | −19.5      | 4.3            | Domestic     | 39.37 | 21.93 | 2.95| 230                    |
| Pig, Sus scrofa domesticus | −20.5      | 4.4            | Domestic     | 39.37 | 21.93 | 2.99| 221                    |
| Pig, Sus scrofa domesticus | −20.5      | 5.1            | Domestic     | 40.18 | 21.47 | 3.05| 225                    |
Table 3. Cont.

| Herbivore                  | δ¹³C | δ¹⁵N | Location     | Lat.  | Lon.  | C/N  | Collagen Yield (mg/g) |
|----------------------------|------|------|--------------|-------|-------|------|-----------------------|
| Pig, *Sus scrofa domesticus* | −19.5| 4.3  | Domestic     | Chalkidiki | 40.51 | 23.63 | 3.10                  | 226                   |
| Pig, *Sus scrofa domesticus* | −20.5| 4.4  | Domestic     | Chalkidiki | 40.51 | 23.63 | 3.11                  | 229                   |
| Pig, *Sus scrofa domesticus* | −20.1| 4.1  | Domestic     | Chalkidiki | 40.51 | 23.63 | 3.08                  | 222                   |
| Pig, *Sus scrofa domesticus* | −23.1| 3.0  | Domestic     | Sparti    | 37.08 | 22.43 | 3.19                  | 224                   |
| Pig, *Sus scrofa domesticus* | −24.1| 2.8  | Domestic     | Sparti    | 37.08 | 22.43 | 3.21                  | 223                   |
| Pig, *Sus scrofa domesticus* | −23.6| 2.6  | Domestic     | Sparti    | 37.08 | 22.43 | 3.07                  | 229                   |
| Pig, *Sus scrofa domesticus* | −23.8| 2.9  | Domestic     | Sparti    | 37.08 | 22.43 | 3.04                  | 228                   |
| Cow, *Bos taurus*           | −21.5| 5.1  | Domestic     | Karditsa  | 39.37 | 21.93 | 2.80                  | 181                   |
| Cow, *Bos taurus*           | −21.4| 5.1  | Domestic     | Attiki    | 37.92 | 23.86 | 2.81                  | 190                   |
| Cow, *Bos taurus*           | −20.9| 4.8  | Domestic     | Attiki    | 37.92 | 23.86 | 2.80                  | 185                   |
| Cow, *Bos taurus*           | −21.2| 5.3  | Domestic     | Attiki    | 37.92 | 23.86 | 2.79                  | 187                   |
| Cow, *Bos taurus*           | −23.2| 3.7  | Domestic     | Sparti    | 37.08 | 22.43 | 2.82                  | 188                   |
| Cow, *Bos taurus*           | −23.0| 3.3  | Domestic     | Sparti    | 37.08 | 22.43 | 2.81                  | 184                   |
| Cow, *Bos taurus*           | −22.9| 3.5  | Domestic     | Sparti    | 37.08 | 22.43 | 2.82                  | 189                   |
| Cow, *Bos taurus*           | −21.7| 5.2  | Domestic     | Karditsa  | 39.37 | 21.93 | 2.81                  | 191                   |
| Cow, *Bos taurus*           | −21.4| 5.6  | Domestic     | Karditsa  | 39.37 | 21.93 | 2.79                  | 183                   |
| Cow, *Bos taurus*           | −21.6| 4.9  | Domestic     | Karditsa  | 39.37 | 21.93 | 2.79                  | 181                   |
| Cow, *Bos taurus*           | −21.3| 5.1  | Domestic     | Karditsa  | 39.37 | 21.93 | 2.80                  | 185                   |
| Cow, *Bos taurus*           | −21.4| 5.8  | Domestic     | Karditsa  | 39.37 | 21.93 | 2.81                  | 186                   |
| Cow, *Bos taurus*           | −21.2| 5.1  | Domestic     | Karditsa  | 39.37 | 21.93 | 2.82                  | 182                   |
| Calf, *Bos taurus*          | −19.2| 9.9  | Domestic     | Karditsa  | 39.37 | 21.93 | 2.80                  | 189                   |
| Horse, *Equus caballus*     | −21.4| 2.6  | Domestic     | Karditsa  | 39.37 | 21.93 | 2.99                  | 171                   |
| Horse, *Equus caballus*     | −20.3| 4.5  | Domestic     | Kozani    | 40.18 | 21.47 | 2.95                  | 169                   |
| Horse, *Equus caballus*     | −18.8| 4.2  | Domestic     | Kozani    | 40.18 | 21.47 | 3.05                  | 173                   |
| Deer, *Capreolus capreolus* | −19.4| 3.1  | Wild         | Kozani    | 40.18 | 21.47 | 3.06                  | 195                   |
| Deer, *Capreolus capreolus* | −19.8| 3.4  | Wild         | Kozani    | 40.18 | 21.47 | 3.11                  | 198                   |
| Carnivore                  |      |      |              |         |       |      |                       |
| Bear, *Ursus Arctos*       | −20.4| 5.2  | Wild         | Kozani    | 40.18 | 21.47 | 3.15                  | 176                   |
| Bear, *Ursus Arctos*       | −20.2| 6.6  | Wild         | Kozani    | 40.18 | 21.47 | 3.19                  | 180                   |
| Bear, *Ursus Arctos*       | −20.2| 6.9  | Wild         | Kozani    | 40.18 | 21.47 | 3.01                  | 177                   |
| Bear, *Ursus Arctos*       | −19.8| 8.7  | Wild         | Kozani    | 40.18 | 21.47 | 3.00                  | 181                   |
| Bear, *Ursus Arctos*       | −21.2| 5.8  | Wild         | Kozani    | 40.18 | 21.47 | 3.10                  | 179                   |
| Bear, *Ursus Arctos*       | −20.6| 6.4  | Wild         | Kozani    | 40.18 | 21.47 | 3.07                  | 176                   |
| Wolf, *Canis lupus*        | −18.5| 10.2 | Wild         | Kozani    | 40.18 | 21.47 | 2.99                  | 200                   |
| Wolf, *Canis lupus*        | −17.0| 10.0 | Wild         | Kozani    | 40.18 | 21.47 | 2.95                  | 202                   |
| Marine low                 |      |      |              |         |       |      |                       |
| Anchovy, *Engraulis encrasicolus* | −17.6| 6.2  | Free–range   |          |       |      |                       |
| Anchovy, *Engraulis encrasicolus* | −18.0| 9.4  | Free–range   |          |       |      |                       |
| Anchovy, *Engraulis encrasicolus* | −17.4| 9.1  | Free–range   |          |       |      |                       |
| Sardene, *Sardina Pilchardus* | −17.1| 6.3  | Free–range   |          |       |      |                       |
| Sardene, *Sardina Pilchardus* | −19.0| 9.0  | Free–range   |          |       |      |                       |
| Sardene, *Sardina Pilchardus* | −18.1| 7.3  | Free–range   |          |       |      |                       |
| Sardene, *Sardina Pilchardus* | −18.5| 8.2  | Free–range   |          |       |      |                       |
Table 3. Cont.

| Herbivore                                      | δ¹³C | δ¹⁵N | Location | Lat. | Lon. | C/N | Collagen Yield (mg/g) |
|------------------------------------------------|------|------|----------|------|------|-----|-----------------------|
| Mussel, *Mytilus galloprovincialis*            | −21.4| 5.3  | Free–range|      |      |     |                       |
| Mussel, *Mytilus galloprovincialis*            | −20.3| 4.7  | Free–range|      |      |     |                       |
| Bogue, *Boops boops*                           | −16.4| 10.6 | Free–range|      |      |     |                       |
| Bogue, *Boops boops*                           | −18.5| 11.2 | Free–range|      |      |     |                       |
| Anchovy, *Engraulis encrasicolus* in olive oil | −24.3| 13.0 | Free–range|      |      |     |                       |
| **Marine high**                                |      |      |           |      |      |     |                       |
| Sargus, *Diplodus sargus*                      | −18.2| 11.7 | Free–range|      |      |     |                       |
| Sargus, *Diplodus sargus*                      | −17.1| 11.5 | Free–range|      |      |     |                       |
| Gilt–head bream, *Sparus aurata*               | −17.5| 11.7 | Fish–farm |      |      |     |                       |
| Gilt–head bream, *Sparus aurata*               | −18.1| 11.3 | Fish–farm |      |      |     |                       |
| Gilt–head bream, *Sparus aurata*               | −13.9| 6.4  | Free–range|      |      |     |                       |
| Mullet, *Mugil Cephalus*                       | −13.8| 7.3  | Free–range|      |      |     |                       |
| Sole, *Solea vulgaris*                         | −18.1| 12.4 | Free–range|      |      |     |                       |
| Red porgy, *Pomatoschistus microps*            | −19.3| 11.1 | Fish–farm |      |      |     |                       |
| Red mullet, *Mugil cephalus*                   | −19.7| 9.4  | Free–range|      |      |     |                       |
| Freshwater Fish                                 |      |      |           |      |      |     |                       |
| Trout, *Salmo trutta*                          | −25.2| 8.4  | Free–range|      |      |     |                       |
| Trout, *Salmo trutta*                          | −23.4| 8.0  | Free–range|      |      |     |                       |
| Common carp, *Cyprinus carpio*                 | −23.5| 12.1 | Free–range|      |      |     |                       |
| Common carp, *Cyprinus carpio*                 | −23.9| 13.3 | Free–range|      |      |     |                       |
| Common carp, *Cyprinus carpio*                 | −24.4| 13.1 | Free–range|      |      |     |                       |
Table 3. Cont.

| Herbivore                          | δ\(^{13}\)C | δ\(^{15}\)N | Location | Lat.  | Lon.  | C/N | Collagen Yield (mg/g) |
|-----------------------------------|-------------|-------------|----------|-------|-------|-----|-----------------------|
| Chicken, Gallus gallus domesticus | −21.8       | 6.4         | Domestic | Kozani| 40.18 | 21.47|                       |
| Duck, Anas platyrhynchos          | −15.5       | 7.5         | Domestic | Kozani| 40.18 | 21.47|                       |
| Duck, Anas platyrhynchos          | −22.7       | 12.0        | Free–range Kozani | 40.18 | 21.47|               |
| Duckling, Anas platyrhynchos      | −26.0       | 8.0         | Domestic | Kozani| 40.18 | 21.47|                       |
| Goose, Anserini sp.               | −18.1       | 9.1         | Domestic | Kozani| 40.18 | 21.47|                       |

Table 4. Isotopic values of Greek plants.

| C\(_3\) Plants                  | δ\(^{13}\)C | δ\(^{15}\)N | Location | Lat.  | Lon.  |
|---------------------------------|-------------|-------------|----------|-------|-------|
| Chios gum, Pistacia lentiscus   | −23.7       | 6.1         | Chios Isl. | 38.26 | 25.97 |
| Chios gum, Pistacia lentiscus   | −23.8       | 6.2         | Chios Isl | 38.26 | 25.97 |
| Propolis                        | −28.7       | 7.0         | Attika   | 38.17 | 23.85 |
| Propolis                        | −28.6       | 7.2         | Attika   | 38.17 | 23.85 |
| Tomato, Solanum lycopersicum   | −28.7       | 7.3         | Ilia     | 37.84 | 21.28 |
| Tomato, Solanum lycopersicum   | −27.9       | 8.3         | Ilia, organic cultivation | 37.84 | 21.28 |
| Orange, Citrus sinensis         | −24.8       | 6.4         | Heraklion, Crete | 35.33 | 25.14 |
| Orange, Citrus sinensis         | −24.9       | 6.3         | Heraklion, Crete | 35.33 | 25.14 |
| Orange, Citrus sinensis         | −25.9       | 5.2         | Sparti   | 37.07 | 22.43 |
| Orange, Citrus sinensis         | −25.9       | 5.0         | Sparti   | 37.07 | 22.43 |
| Orange, Citrus sinensis         | −26.1       | 4.8         | Sparti   | 37.07 | 22.43 |
| Orange, Citrus sinensis         | −25.2       | 5.5         | Sparti   | 37.07 | 22.43 |
| Orange, Citrus sinensis         | −25.8       | 4.2         | Peloponisos, Kiato | 38.01 | 22.75 |
| Orange, Citrus sinensis         | −26.1       | 2.1         | Peloponisos, Kiato | 38.01 | 22.75 |
| Orange, Citrus sinensis         | −26.8       | 1.9         | Peloponisos, Kiato | 38.01 | 22.75 |
| Peach, Prunus persica           | −26.1       | 2.0         | Peloponisos, Kiato | 38.01 | 22.75 |
| Peach, Prunus persica           | −25.9       | 1.9         | Peloponisos, Kiato | 38.01 | 22.75 |
| Peach, Prunus persica           | −25.5       | 1.3         | Peloponisos, Kiato | 38.01 | 22.75 |
| Peach, Prunus persica           | −25.4       | 2.2         | Peloponisos, Kiato | 38.01 | 22.75 |
| Peach, Prunus persica           | −26.7       | 1.4         | Naousa   | 40.63 | 22.07 |
| Peach, Prunus persica           | −26.6       | 0.2         | Naousa   | 40.63 | 22.07 |
| Peach, Prunus persica           | −25.8       | −1.1        | Naousa   | 40.63 | 22.07 |
| Grape, Vitis vinifera           | −26.2       | 3.8         | Amynteo  | 40.69 | 21.68 |
| Grape, Vitis vinifera           | −25.3       | 3.6         | Nemea    | 37.82 | 22.66 |
| Honey                           | −25.1       | 1.8         | Chalkidiki | 40.42 | 23.50 |
| Honey                           | −24.9       | 1.8         | Vittina, Arkadia | 37.67 | 22.18 |
| Honey                           | −25.9       | 1.6         | Sparti   | 37.07 | 22.43 |
| Honey                           | −26.0       | 1.6         | Sparti   | 37.07 | 22.43 |
| Honey                           | −25.6       | 1.8         | Sparti   | 37.07 | 22.43 |
| Honey                           | −26.1       | 2.0         | Sparti   | 37.07 | 22.43 |
| Honey                           | −26.1       | 2.1         | Kithira  | 36.24 | 22.99 |
| C3 Plants                  | $\delta^{13}$C | $\delta^{15}$N | Location    | Lat.  | Lon.  |
|----------------------------|----------------|----------------|-------------|-------|-------|
| Honey                      | −26.3          | 2.1            | Kithira     | 36.24 | 22.99 |
| Honey                      | −27.0          | 1.9            | Kithira     | 36.24 | 22.99 |
| Honey                      | −25.4          | 1.3            | Attiki      | 37.98 | 23.73 |
| Chestnut, Castanea sativa | −27.4          | 2.4            | Domnista    | 38.58 | 21.85 |
| Chestnut, Castanea sativa | −27.2          | 2.0            | Domnista    | 38.58 | 21.85 |
| Chestnut, Castanea sativa | −27.1          | 1.6            | Domnista    | 38.58 | 21.85 |
| Chestnut, Castanea sativa | −27.0          | 1.7            | Domnista    | 38.58 | 21.85 |
| Chestnut, Castanea sativa | −27.3          | 2.1            | Domnista    | 38.58 | 21.85 |
| Chestnut, Castanea sativa | −27.3          | 3.7            | Domnista    | 38.58 | 21.85 |
| Chestnut, Castanea sativa | −26.9          | 3.9            | Domnista    | 38.58 | 21.85 |
| Cercis                     | −27.4          | 3.3            | Parnitha    | 38.13 | 23.81 |
| Cercis                     | −27.3          | 3.4            | Parnitha    | 38.13 | 23.81 |
| Cercis                     | −27.5          | 3.5            | Parnitha    | 38.13 | 23.81 |
| Cercis                     | −27.3          | 2.6            | Parnitha    | 38.13 | 23.81 |
| Cercis                     | −27.6          | 3.0            | Parnitha    | 38.13 | 23.81 |
| Cercis                     | −27.2          | 3.2            | Parnitha    | 38.13 | 23.81 |
| Plane tree, Plataneus orientalis | −30.1 | 2.1              | Parnitha    | 38.13 | 23.81 |
| Plane tree, Plataneus orientalis | −29.1 | 2.3              | Parnitha    | 38.13 | 23.81 |
| Plane tree, Plataneus orientalis | −28.9 | 2.4              | Parnitha    | 38.13 | 23.81 |
| Plane tree, Plataneus orientalis | −28.9 | 2.2              | Parnitha    | 38.13 | 23.81 |
| Plane tree, Plataneus orientalis | −26.4 | 3.8              | Parnitha    | 38.13 | 23.81 |
| Plane tree, Plataneus orientalis | −28.2 | 2.8              | Parnitha    | 38.13 | 23.81 |
| Plane tree, Plataneus orientalis | −27.8 | 2.5              | Parnitha    | 38.13 | 23.81 |
| Pine tree, Pinus Pinea    | −28.8          | 10.6           | Parnitha    | 38.13 | 23.81 |
| Pine tree, Pinus Pinea    | −28.5          | 11.0           | Parnitha    | 38.13 | 23.81 |
| Pine tree, Pinus Pinea    | −29.1          | 9.8            | Parnitha    | 38.13 | 23.81 |
| Oak, Quercus sp.          | −28.2          | 0.0            | Domnista    | 38.58 | 21.85 |
| Oak, Quercus sp.          | −28.7          | 0.1            | Domnista    | 38.58 | 21.85 |
| Oak, Quercus sp.          | −28.5          | 0.6            | Domnista    | 38.58 | 21.85 |
| Oak, Quercus sp.          | −28.5          | 0.5            | Domnista    | 38.58 | 21.85 |
| Oak, Quercus sp.          | −28.0          | 0.7            | Domnista    | 38.58 | 21.85 |
| Oak, Quercus sp.          | −28.3          | 0.4            | Domnista    | 38.58 | 21.85 |
| Mallow tree, Malva sylvestris | −29.1 | 8.4              | Parnitha    | 38.13 | 23.81 |
| Mallow tree, Malva sylvestris | −28.7 | 7.9              | Parnitha    | 38.13 | 23.81 |
| Mallow tree, Malva sylvestris | −29.3 | 8.8              | Parnitha    | 38.13 | 23.81 |
| Olive tree, Olea europea  | −26.5          | 7.4            | Parnitha    | 38.13 | 23.81 |
| Olive tree, Olea europea  | −26.3          | 7.1            | Parnitha    | 38.13 | 23.81 |
| Olive tree, Olea europea  | −25.9          | 6.8            | Parnitha    | 38.13 | 23.81 |
| Chios gum, Pistacia lentiscus | −28.5 | 9.4              | Parnitha    | 38.13 | 23.81 |
| Walnut tree, Juglans regia | −28.4          | 1.3            | Karpenisi   | 38.92 | 21.78 |
| Walnut tree, Juglans regia | −28.0          | 2.1            | Karpenisi   | 38.92 | 21.78 |
Table 4. Cont.

| C3 Plants                  | δ¹³C | δ¹⁵N | Location | Lat.  | Lon.  |
|----------------------------|------|------|----------|-------|-------|
| Hazel tree, *Corylus avellana* | −27.7 | 1.1  | Karpenisi | 38.92 | 21.78 |
| Hazel tree, *Corylus avellana* | −28.1 | 1.7  | Karpenisi | 38.92 | 21.78 |
| Crocus, *Crocus sativus*     | −26.1 | 1.3  | Kozani    | 40.30 | 21.79 |
| Crocus, *Crocus sativus*     | −26.3 | 1.2  | Kozani    | 40.30 | 21.79 |
| Crocus, *Crocus sativus*     | −25.9 | 1.2  | Kozani    | 40.30 | 21.79 |
| Crocus, *Crocus sativus*     | −25.9 | 1.5  | Kozani    | 40.30 | 21.79 |
| Spruce, *Picea abies*        | −30.2 | 3.4  | Attiki    | 37.98 | 23.73 |
| Pine tree, *Pinus Pinea*     | −27.1 | 3.7  | Attiki    | 37.98 | 23.73 |
| Olive tree, *Olea europea*   | −28.1 | −4.5 | Criti, Irakleio | 35.33 | 25.07 |
| Olive tree, *Olea europea*   | −28.6 | −4.3 | Criti, Irakleio | 35.33 | 25.07 |
| Olive tree, *Olea europea*   | −27.4 | −4.1 | Criti, Irakleio | 35.33 | 25.07 |
| Olive tree, *Olea europea*   | −28.3 | −4.2 | Criti, Irakleio | 35.33 | 25.07 |
| Olive tree, *Olea europea*   | −28.4 | 2.1  | Criti, Chania | 35.52 | 24.02 |
| Olive tree, *Olea europea*   | −28.3 | 2.2  | Criti, Chania | 35.52 | 24.02 |
| Olive tree, *Olea europea*   | −29.7 | 4.3  | Analipsi, Messinia | 37.02 | 21.97 |
| Olive tree, *Olea europea*   | −29.3 | 3.4  | Analipsi, Messinia | 37.02 | 21.97 |
| Olive tree, *Olea europea*   | −30.1 | 1.2  | Vasilada, Messinia | 37.09 | 21.94 |
| Olive tree, *Olea europea*   | −29.2 | 1.1  | Velika, Messinia | 37.01 | 21.93 |
| Olive tree, *Olea europea*   | −28.9 | 1.7  | Diodia, Messinia | 37.08 | 21.86 |
| Olive tree, *Olea europea*   | −28.8 | 2.6  | Lykotrafas, Messinia | 37.05 | 21.95 |
| Olive tree, *Olea europea*   | −29.3 | 2.1  | Lykotrafas, Messinia | 37.05 | 21.95 |
| Olive tree, *Olea europaea*  | −29.4 | 1.1  | Madena, Messinia | 37.04 | 21.96 |
| Olive tree, *Olea europaea*  | −29.4 | 2.8  | Neochori, Messinia | 37.03 | 21.92 |
| Olive tree, *Olea europaea*  | −29.9 | −0.2 | Neochori, Messinia | 37.03 | 21.92 |
| Olive tree, *Olea europaea*  | −28.6 | 4.1  | Polyalistra, Messinia | 37.07 | 21.97 |
| Olive tree, *Olea europaea*  | −29.8 | 4.0  | Polyalofos, Messinia | 37.09 | 21.91 |
| Olive tree, *Olea europaea*  | −29.7 | −1.2 | Strefi, Messinia | 37.05 | 21.89 |
| Olive tree, *Olea europaea*  | −29.5 | 4.3  | Avramio, Messinia | 37.03 | 22.03 |
| Olive tree, *Olea europaea*  | −28.7 | 3.5  | Avramio, Messinia | 37.03 | 22.03 |
| Olive tree, *Olea europaea*  | −29.1 | 1.1  | Avramio, Messinia | 37.03 | 22.03 |
| Olive tree, *Olea europaea*  | −29.6 | 3.2  | Messini, Messinia | 37.05 | 22.01 |
| Olive tree, *Olea europaea*  | −26.9 | −1.5 | Nemea     | 37.82 | 22.66 |
| Olive tree, *Olea europaea*  | −25.3 | −1.0 | Nemea     | 37.82 | 22.66 |
| Olive tree, *Olea europaea*  | −26.9 | −1.1 | Nemea     | 37.82 | 22.66 |
| Olive tree, *Olea europaea*  | −26.7 | −1.2 | Nemea     | 37.82 | 22.66 |
| Olive tree, *Olea europaea*  | −26.3 | −1.2 | Nemea     | 37.82 | 22.66 |
| Olive tree, *Olea europaea*  | −26.6 | −1.5 | Nemea     | 37.82 | 22.66 |
| Table 4. Cont. | C3 Plants | $\delta^{13}C$ | $\delta^{15}N$ | Location | Lat. | Lon. |
|---|---|---|---|---|---|---|
| Olive tree, *Olea europea* | −26.7 | −1.5 | Nemea | 37.82 | 22.66 |
| Wheat, *Triticum dicoccum* | −25.3 | 2.3 | Phthiotis | 38.90 | 22.53 |
| Wheat, *Triticum dicoccum* | −24.0 | 3.0 | Phthiotis | 38.90 | 22.53 |
| Rye, *Secale cereale* | −24.2 | 3.4 | Phthiotis | 38.90 | 22.53 |
| Oat, *Avena sativa* | −28.6 | 2.6 | Phthiotis | 38.90 | 22.53 |
| Chickpea, *Cicer arietinum L.* | −25.2 | 2.9 | Phthiotis | 38.90 | 22.53 |
| Linen, *Linum sp.* | −27.8 | 5.8 | Phthiotis | 38.90 | 22.53 |
| Grass pea, *Lathyrus sativus L.* | −24.6 | 1.3 | Phthiotis | 38.90 | 22.53 |
| Lentil, *Lens culinaris* | −24.7 | 2.0 | Phthiotis | 38.90 | 22.53 |
| Mung bean, *Vigna radiata* | −20.7 | 0.1 | Phthiotis | 38.90 | 22.53 |
| Green Bean, *Phaseolus vulgaris* | −25.8 | 2.3 | Phthiotis | 38.90 | 22.53 |

| C4 Plants | $\delta^{13}C$ | $\delta^{15}N$ | Lat. | Lon. |
|---|---|---|---|---|
| *Zea mays* | −12.2 | 4.0 | Macedonia, Ptolemaida | 40.51 | 21.68 |
| Corn, *Zea mays* | −13.1 | 5.0 | Macedonia | 40.75 | 22.90 |
| Corn, *Zea mays* | −12.8 | 5.2 | Macedonia | 40.75 | 22.90 |
| Corn, *Zea mays* | −13.8 | 6.1 | Macedonia | 40.75 | 22.90 |
| Corn, *Zea mays* | −12.8 | 5.6 | Macedonia | 40.75 | 22.90 |
| Corn, *Zea mays* | −12.9 | 5.2 | Macedonia | 40.75 | 22.90 |
| Corn, *Zea mays* | −13.2 | 5.3 | Macedonia | 40.75 | 22.90 |
| Corn, *Zea mays* | −13.6 | 6.0 | Macedonia | 40.75 | 22.90 |
| Corn, *Zea mays* | −12.8 | 5.9 | Macedonia | 40.75 | 22.90 |
| Mosses, *Bryophyta* | −12.1 | 8.2 | Kechries, Corinth | 37.88 | 22.99 |
| Mosses, *Bryophyta* | −10.0 | 5.5 | Pidna | 40.39 | 22.56 |
| Mosses, *Bryophyta* | −12.2 | 4.9 | Anavissos | 37.73 | 23.94 |
| Mosses, *Bryophyta* | −12.0 | 11.5 | Agathoupoli | 40.46 | 22.58 |

**Palaeodiet**

The $\delta^{13}C$ and $\delta^{15}N$ values of human bone collagen as published in the literature covering the Early Neolithic, Late Neolithic, Early Bronze, Middle Bronze and Late Bronze period are presented in Figure 2. In the same Figure 2e we also present $\delta^{15}N$ and $\delta^{13}C$ values of human hair from contemporary Greek population (Table 2). These hair ceratin values were converted to bone collagen values according to O’Connell (2001) [74]. The red rectangles in all cases represent the isotopic values for human bones consuming extreme diets (marine high, marine low, herbivore, carnivore) as indicated in Richards and Hedges 1999 [75]. Specifically, for Figure 2a–d the values are deducted from fauna samples from the archaeological sites [17,49–51,59,61,63,67] for Early/Late Neolithic, Early Bronze, Middle Bronze and Late Bronze periods, respectively. For Figure 2e the red rectangle are values as deducted from Tables 3 and 4. The values used in Figure 2 for the red rectangles are summarized in Table 5 where all the conversions are indicated analytically. The “C3 plant diet” is the mean value of all herbivore isotopic data of each period, the “carnivore diet” is the value of the mean herbivore adjusted by one trophic level for each period and the “marine diet” is the value of the mean marine isotopic data of each period adjusted by one trophic level. For Figure 2e the “low/high marine diet” are the mean values of the low/high marine isotopic data of Table 3, after converted to bone and after adjusted by one trophic level.
Figure 2. (a–d) δ^{15}N and δ^{13}C values of human bone collagen as published in the literature covering the Neolithic (EN: Early Neolithic, LN: Late Neolithic), Early Bronze, Middle Bronze and Late Bronze age, respectively. (e) δ^{15}N and δ^{13}C values of human hair samples of contemporary Greek population. The red rectangles indicate the theoretical isotopic values of human bone of a subject under 100% herbivore (lower left), 100% carnivore (upper left) and 100% marine diet (right low/high for low marine and high marine respectively). The values were deducted from fauna of the respectively periods and archaeological sites, as published in the literature and for (e) from measurements of contemporary Greek food sources (Tables 3 and 4).
Table 5. Theoretical Isotopic values of human bones under extreme diets.

| δ13C (Human Bone) | Neolithic (Early/Late) | EBA | MBA | LBA | Recent |
|-------------------|------------------------|-----|-----|-----|--------|
| #marine low diet  | -                      | -   | -   | -   | −13.4 * |
| C3 plant diet     | −20.3/−20.1            | −20.0 | −20.1 | −20.1 | −21.5 |
| Carnivore diet    | −19.3/−19.1            | −19.0 | −19.1 | −19.1 | −20.5 |
| marine high diet  | −12.4/−12.4            | −11.0 | −9.6 | −17.3 | −12.4 * |

| δ15N (Human Bone) | Neolithic | EBA | MBA | LBA | Recent |
|-------------------|-----------|-----|-----|-----|--------|
| #marine low diet  | -         | -   | -   | -   | 10.9 * |
| C3 plant diet     | 5.3       | 5.8 | 4.5 | 4.7 | 5.0 |
| Carnivore diet    | 7.7       | 8.8 | 7.5 | 7.7 | 8.0 |
| marine high diet  | 11.0      | 11.0 ** | 11.0 | 10.7 | 13.5 * |

* The flesh values of Table 3 were adjusted to bone collagen values by adding 4‰ to the δ13C values. ** No archaeological data of low fish were available. * The marine high fish for the EBA period is the intermediate value from Neolithic to MBA due to lack of archaeological fauna samples of the period.

Human isotope values of δ13C range for Early Neolithic from −20.5‰ to −17.8‰ (Figure 2a). For Late Neolithic from −20.7‰ to −17.9‰ (Figure 2a), for EBA (Figure 2b) from −21.4‰ to −18.4‰, for MBA (Figure 2c) from −20.6‰ to −18.4‰, for LBA (Figure 2d) from −21.7‰ to −17.8‰ and for the recent Greek population (Figure 2e), after applying the conversion from ceratin hair to bone collagen [74], from −20.4‰ to −18.6‰. The δ15N human isotope values range from 6.7‰ to 10.4‰ (Early Neolithic), from 5.6‰ to 10.6‰ (Late Neolithic), 7.2‰ to 10.0‰ (EBA), 7.2‰ to 10.8‰ (MBA), 6.1‰ to 11.5‰ (LBA) and 8.5‰ to 10.4‰ (Recent).

According to the results presented in Figure 2, the diet of the residents of ancient Greece is dominated by terrestrial plant foods and meat with the addition of variable minor amounts of fish. Furthermore, we can observe a possible contribution of marine protein in Neolithic and Late Bronze age, in specific sites (Fratchi and Kefalas for Neolithic and Almyri, Kritika, Pineiada, and Rymnio for Late Bronze age), as their isotopic values are located to the right upper side of the red rectangle in Figure 2a,d respectively. For the EBA and MBA the marine protein consumption is not likely or inconclusive (for the EBA—Asine site [63]). Another general observation from Figure 2 is that the vast majority of the human isotopic values are outside the red rectangles, especially for the EBA (Figure 2b). This is a strong indication that the model of the four extreme diet sources [75] is not complex enough in order to accurately explain the isotopic values of the human samples. This is especially evident in the case of recent humans (2e) where the red rectangle was derived from contemporary Greek food sources. In Figure 3 we present the mean values of the human collagen bones for all the periods (the values for the recent human samples were corrected by adding 1.5‰ in the 13C value in order to account the Suess effect) along with all the archaeological fauna samples of the periods, (Figure 3a) as extracted from the literature and all recent Greek food sources (Figure 3b). All the values of the terrestrial Greek food sources were corrected to the Suess effect and the flesh samples were converted to bone collagen (see methodology section). The scales of Figure 3a,b are kept the same to facilitate comparison. There are not major variations in the absolute values of foods in Figure 3a,b indicating that both can be used as food database for palaeodiet reconstructions. Thus, if we include more food sources (like freshwater fish and birds) the interpretation of the isotopic values of Figure 2 (data from literature) or Figure 3b (mean values of the literature data) is more pleasing.

The human collagen samples are, in general, enriched in both 13C and 15N in comparison to the herbivores for all studied periods (Figure 3a). The mean human δ13C (−19.4‰ for Early Neolithic, −19.7‰ for Late Neolithic, −19.7‰ for EBA, −19.8‰ for MBA and −19.9‰ for LBA) are higher than the mean faunal herbivores values by 0.9‰ for Early Neolithic, 0.4‰ for Late Neolithic, 0.3‰ for EBA, 0.4‰ for MBA and 0.2‰ for LBA). The mean human δ15N (8.2‰ for Early Neolithic, 8.1‰ for Late Neolithic, 9.2‰ for EBA, 8.5‰ for MBA and 7.4‰ for LBA) are higher than the mean herbivores
fauna values by 2.9‰ for Early Neolithic, 2.8‰ for Late Neolithic 3.4‰ for EBA, 4.0‰ for MBA and 2.7‰ for LBA. This is consistent with a trophic level and demonstrates the importance of terrestrial meat sources in the diet while one must retain in mind the possible influences to these values by the consumption of dairy products or manuring practices [76].

![Figure 3](image)

**Figure 3.** Mean isotopic values of human bone collagen for all the periods studied in relation to the food webs (a) archaeological samples, (b) modern Greek foods from Table 3; Table 4 after applying the Suess effect correction to terrestrial samples and converting flesh samples to bone.

Humans living in the Greek mainland during the Neolithic are slightly enriched in δ13C over human Neolithic bones from the continental Europe (Bocherens et al., 2007) [76], which are usually between −20‰ and −21‰. This difference in δ13C values is attributable to both climatic variations and diet. Studies of wood, charcoal, and bone samples from European archaeological sites have shown that δ13C tends to become enriched in a north to south direction, following the climatic/temperature gradient toward the Mediterranean [77]. The δ15N values of the Neolithic Greek human bones are in general lower than the values of human Neolithic bones from the continental Europe [76] which are usually between 9.0‰ and 10.4‰ [76]. Only the δ15N bones found at coastal and island Neolithic sites (Fragthi and Kefala) have values similar to the ones of the continental Europe. This suggests that these humans were obtaining a detectable amount [57,78] of their dietary protein from marine sources (more than 20% in Fragthi and Kefala) and these fish consumption depends on the location of the individual.

Previous isotopic analyses of European coastal populations [79,80] have revealed a linear correlation between δ15N and δ 13C values within an area defined by terrestrial and marine (δ 13C, δ15N) values suggesting that individuals were eating varying proportions of terrestrial and marine foods [79]. In Figure 4 we present the isotopic values of human bones collagen from the referred archaeological sites versus the fauna baselines of the sites both terrestrial and marine (rectangles T and M respectively). The ranges of the fauna baselines are given in Table 6.

| δ13C %‰  | Early Neolithic | Late Neolithic | EBA | MBA | LBA |
|----------|-----------------|----------------|-----|-----|-----|
| Terrestrial | −21.9 to −18.0  | −21.7 to −17.3 | −20.7 to −19.5 | −21.2 to −19.1 | −23.2 to −16.9 |
| Marine   | −14.7 to −9.3   | −12.0 to −9.2  | −16.5 to −10.1 |
| δ15N %‰  | Early Neolithic | Late Neolithic | EBA | MBA | LBA |
| Terrestrial | 6.8 to 3.8      | 8.5 to 3.2     | 7.5 to 3.4 | 5.8 to 3.4 | 7.1 to 3.4 |
| Marine   | 9.2 to 3.6      | 9.2 to 6.8     | 11.6 to 6.1 |
In Figure 4 we also overlap the food database (circles) of Figure 3b. In the MBA period of Figure 4 we can see that the rectangles (T and M) have almost the same boundaries with the corresponding circles of the food database (the herbivore and low/high marine circles). Contrary, in the LBA period of Figure 4, the rectangles (T and M) have considerably shorter boundaries than the corresponding food database circles as well as to the rectangles of the other periods (MBA and Neolithic). This may relate to the lack of adequate number of ancient fauna samples of the period (marine samples) and could lead to erroneous interpretations of the palaeodiet. By considering the food database circles (especially the extent of the herbivore circle) a more accurate interpretation may be visualized. For the EBA period there is no ancient marine sample available (no M rectangle in Figure 4) to establish the isotopic marine baseline and we have to solely rely on the food database circles in order to determine possible contribution of marine protein in the diet for that period.

The data from the Neolithic sites of Fragthi and Kefala (Figure 4) are consistent with the consumption of at least some marine protein challenging the general idea that during the Neolithic there was no signal of marine sources in the human diet [49–51] and agrees with the finding of modest numbers of fish in the deposits of Neolithic settlements of N. Greece [49–51]. In the rest of the Neolithic sites the isotopic analysis of human remains revealed a diet that included a significant proportion of foods based on C3 plants and the bulk of the dietary protein must have been provided by terrestrial mammals, either hunted wild mammals or husbanded domestic mammals [18]. The lower δ¹⁵N which was found in some human bones (Alepotrypa) suggest consumption of legumes that have extremely low δ¹⁵N [18].
A detectable [67,78] (≥20%) contribution of marine diet is also observed for the LBA sites of Almyri, Pineiada, Rymnio and Kritika (their mean δ\(^{15}\)N are 9.3‰, 9.1‰, 8.9‰ and 9.3‰, respectively). It is not possible to determine the marine contribution with less than ±10 % accuracy. For example, if we assume a mean δ\(^{15}\)N value equal to 8‰ for terrestrial diet and 11‰ for marine diet, the mass equation for the cases of (i.) 80% terrestrial + 20% marine diet (ii.) 70% terrestrial + 30% marine diet and (iii.) 60% terrestrial + 40% marine diet, yield δ\(^{15}\)N values equal to 8.6‰, 8.9‰ and 9.2‰ respectively. These values are close to the reported mean values for the above four regions but seem unrealistic, underlying that the model of the four basic food sources (C3 plants, herbivores, marine high/low) [75] is not complex enough to explain the human diet. In addition, even though it is easy to justify the contribution of marine foods in the population of Almyri and Kritika that are coastal or near coastal areas, it is difficult to imagine fish consumption in Rymnio and Pinaida, since these are inland sites. For these two areas, the enrichment in N isotope may be connected to consumption of dairy products or birds or even foraging of nearby large rivers (e.g., river Aliakmon, near Rymnio) in search of freshwater animals that have more positive δ\(^{15}\)N values than their terrestrial counterparts.

For the EBA sites (Manika and Perachora) our analysis does not detect marine protein contrary to the bibliography that suggests a mixed diet of C3 with marine resources/few fish.

For the MBA sites, while our analysis agrees with the literature findings for Koufovounou (C3 consumption with legumes), for the sites of Argos and especially Asine, the fish contribution to diet seems detectable.

5. Conclusions

The results of the Neolithic populations revealed a diet that included a significant proportion of foods based on C3 plants and the bulk of the dietary protein must have been provided by terrestrial mammals with a small but detectable proportion of marine protein for coastal (Fragthi—Argolida) and Island (Kefala—Kea) populations. A detectable contribution of marine diet is observed in Almyri, Perahora, Rymnio and Kritika (Late Bronze age) populations. Further, the enrichment in both N isotopes maybe connected, for some areas, to freshwater consumption. In the rest of the sites the isotopic analysis of human remains revealed a diet that included a significant proportion of foods based on C3 plants and the bulk of the dietary protein must have been provided by terrestrial mammals. The isotopic values of the MBA sites of Argos and Asine seem to justify a detectable consumption of fish.

A database consisting of foods from the general territory of Greece was presented. The isotopic values of this database were compared to the available fauna bone collagen data from the archaeological sites reviewed in this study. No significant differences are observed and this database, in our opinion, may be used as a baseline for palaeodiet studies for the Neolithic and Bronze Age in Greece.

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