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# A stochastic approach to the reconstruction of prehistoric human diet in the Pacific region from bone isotope signatures

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**ABSTRACT:** A theoretical constraint on dietary reconstructions using isotope analyses of human bones is that for a given number of isotopes, N, one cannot calculate the proportions of more than N+1 food types. This strict algebraic limitation can be relaxed by adopting a stochastic approach, recommended by Minagawa (1992). This strategy is investigated for prehistoric diet in the South Pacific region, focusing on seven of the main food types available to these people: C3 plants, C4 plants, land herbivores, marine shellfish, coral reef fish, non-reef fish, and marine mammals.

Sixty-three underlying assumptions were identified and examined in detail. These consist of the mean values for each food type of protein, energy, $\delta^{13}C$, $\delta^{15}N$, $^{34}S$; the offset values for each isotope from the food to human bone collagen; fractionation effects from flesh to collagen in animals; and acceptable daily intake ranges for protein and energy in human diet. Because of the complexity of environmental regimes in the Pacific it was also found necessary to tabulate these assumptions into two groups: one set of assumptions relevant to prehistoric people whose environment is dominated by maritime conditions, such as atolls, and a second set where the land is the dominant influence.

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A computer simulation algorithm is developed which is based on Minagawa's method. This was tested using a 'Reverse Experiment' procedure. By taking a diet of known percentage weight composition the isotope composition of human bone was forward calculated from this diet. The algorithm was then employed on this isotope signature to see if the original food composition could be calculated in reverse. The differences between real and calculated food weight percentages for the seven foods were 4.8, 0.1, 4.5, 1.8, 1.5, 1.8 and 1.4% respectively. These were all within acceptable statistical limits. Using the full set of assumptions it was then tested on isotope results for $\delta^{13}C$, $\delta^{15}N$ and $^{34}S$ for a prehistoric Pacific group from the Chatham Islands.

## INTRODUCTION

There is now considerable published material relating to the reconstruction of ancient diet from isotope signatures obtained from human bone collagen. These studies followed on from the recognition that $\delta^{13}C$ values varied considerably from one food to another, and in particular were substantially different from marine to land foods. However, it was soon realised that several quite different kinds of diet could produce the same overall $\delta^{13}C$ isotope signature in human bone. For example, one prehistoric community might possess a mean value of $\delta^{13}C$ of -10‰ because they relied heavily on marine foods, while another group might have the same mean value with little or no marine food in their diet, but significant amounts of C4 plants, which have $\delta^{13}C$ values in the vicinity of -10‰.

Soon after this form of diet discrimination began to be investigated, a second isotope, $^{15}N$, was introduced to the research field. This is an isotope which also fractionates in nature, and therefore could be used to trace reliance on different kinds of food. Some of the ambiguities involved with $^{13}C$ could be resolved by the addition of this second isotope. Here too, however, further ambiguities were soon found. A strongly terrestrial diet could result in a signature of say $\delta^{15}N$ +7‰ and a strongly marine focus in say $\delta^{15}N$ = +20‰; however, a group strongly reliant on foods from inshore coral reefs would appear to have had a dietary focus on land-based foods because reef animals can have $\delta^{15}N$ values around the +5‰ range.

It is readily apparent from this that neither univariate nor bivariate isotope characterisation in this field can adequately solve the ambiguities mentioned. This difficulty in interpreting causes from effects, which is fundamental in archaeology, has been dubbed 'the problem of equifinality' (Torrence 1986: 21-22, Torrence *et al.* 1992), but could also be referred to as 'the problem of multi-causality'. This type of problem is prevalent in archaeology; for example, it is present in the trace element characterisation of obsidians, where multiple-element signatures are used to work backwards and identify geological sources from this information (Leach and Manly, 1982). Indeed,

there is a close parallel which could be drawn between the desire to characterise diets with trace elements and isotopes, and obsidian characterisation research. A few useful hints might be gained from the history of research on the obsidian problem. In general, the more elements one can use the better the characterisation will be. That is, so long as one uses multivariate mathematical techniques appropriate to the multi-element nature of the problem. The word 'element', in this respect, should be thought of in a generic sense of 'elements of information', rather than simply referring to an element in the Periodic Table. For example, if we can add information from say the natural radioactive emissions from obsidian artefacts, in addition to elemental characterisation, then some further source ambiguities may be solved (Leach *et al.* 1978).

In diet research too, it would be advisable to lean on as many sources of information as one can, if one is reliably to discover what kind of cause (diet) produced a certain effect (isotope signature). In the short history of isotope research and human diet, there seems to have been very little willingness to do this; almost all scholars adopting either a univariate or at most bivariate approach, and employing relatively simple mathematical modelling. A novel extension to this process of expanding the information base has been to incorporate the results from classical midden analysis into the interpretation of isotope signatures (Minagawa and Akazawa, 1989: 10-11; 1992), by, in effect, placing certain Boolean filters in the path of interpretation. In its simplest form, this would work along these lines—if one is investigating the diet of a group of highland people from Papua New Guinea, one is justified in ignoring the ambiguity created by the $^{15}N$ signature of coral reef biota. This suggests adopting a more flexible approach when interpreting cause from effect in this field, and using a mixture of common sense Boolean logic as well as multivariate modelling[1].

In a recent paper by Schwarcz (1991) it was argued that there is a strict theoretical limit to how many sources of food (causes) can be reconstructed from a certain number of isotope ratios (effects). This is simply stated as:

> "Using analyses of a given number, N, of isotope elements (C, N, H, O, etc.) it is possible in principle to estimate the proportions of N+1 dietary compositions of known, well defined isotopic composition. For maximum effectiveness, any isotopic palaeodiet study should be preceded by an archaeological, archaeo-botanical and -zoological study to define the lists of foods that were actually consumed" (Schwarcz, 1991: 273).

This strict theoretical limitation only applies in the case of what Minagawa has called the 'analytic feeding model' where an exact algebraic solution is sought (Minagawa,

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[1]An example of a boolean filter in the algorithm would be — if the prehistoric group was resident in a region without C4 plants in the environment, then the part of the algorithm which calculates the contribution of C4 plants from the collagen $\delta^{13}C$ value can be ignored.

1992: 146-147). This requirement is unnecessarily harsh, and he suggests that it is possible to reconstruct <N+1 dietary constituents from N isotopes, if one takes a somewhat more relaxed stochastic approach to the matter, and sacrifices exact solutions in favour of probable ones. This seems a perfectly reasonable suggestion, given the wide range of uncertainties and sources of variation in this whole field. There are basically two ways of adopting this more relaxed strategy:

> **Model 1:** Forward calculate the isotope values which would result from consuming all possible proportions of a series of food categories specified, and then check the archaeological bone isotope signature against these results to see what food proportions may have produced it.
>
> **Model 2:** Randomly choose proportions of the series of foods specified, calculate the isotope signature which would result from such a diet, and check the archaeological signature against this. If there is a reasonable match then store this away as one possible solution. After a period of such simulations, the various solutions can be examined to determine their ranges, and central tendencies (if any).

The first approach would involve formidable computing, and Minagawa suggests following the latter course, and even in this case advises introducing some Boolean logic, such as rejecting dietary solutions which satisfy the model, but which would be unacceptable for human health, such as those which are outside the demands of human metabolism for protein and energy.

The suggestions by Minagawa seem very sensible to us, and we decided to incorporate them in a study which is underway of prehistoric diet in the Pacific region. In essence this involves developing suitable software for simulating diets and forward calculating possible isotope signatures, given the range of basic food types available to Pacific peoples. An attempt to adopt Model 1 failed through lack of computer power, although this will be investigated in future. Minagawa's algorithm has been applied to prehistoric communities in Japan, but since the foods in Japan are quite different to those available in Oceania we need to adapt the model to these different conditions. We also felt that Minagawa had not fully explored the entire range of assumptions which are involved in the model, and this subject forms a substantial part of this paper.

The first thing which is necessary is to identify all the assumptions which are involved in the process of reconstructing a diet from an isotope signature from human bone collagen. For example, reasonable values need to be identified for such things as an average $\delta^{13}C$ value for C4 plants. After carefully examining all the premises involved, we found as many as 63 assumptions which must be used in the simulation algorithm. The values chosen for each of these is discussed and documented below.

It was also found necessary to formulate not one but two sets of assumptions, depending on the soil chemical environment of the population of people being studied.

This arises from the rather special environmental circumstances which many Pacific islanders find themselves in — with soils which wholly or largely derive from marine sediments. These soils, the plants which grow on them, and the animals which browse on these plants have different isotope signatures than in a regime where soils derive from non-marine sediments. Humans living in these two different regimes will have quite different isotope signatures even if they had identical diets. Thus, the Table of assumptions used for the people of Kapingamarangi who live on an atoll will be quite different to the Table used for the Nebira people who lived inland in Papua New Guinea. These two Tables will be referred to as the *Marine Dominated Assumptions* and the *Land Dominated Assumptions* respectively.

A total of seven main food types are used in the simulation software, and these constitute the rows in two final tables which summarise the assumptions (Tables 2 and 3). These food-types are as follows:

1 = C3 Plants
2 = C4 Plants
3 = Land Herbivores
4 = Marine Shellfish
5 = Coral Reef Fish
6 = Non-Reef Fish
7 = Marine Mammals

In each table, there are eight columns, representing the different assumptions which need to be made, making a sub-total of 56. There are an additional seven assumptions required (see base of Table 1), bringing the total to 63. These are listed below, together with the "Assumption Number" for each cell. It will be convenient at times in the discussion which follows to use these numbers as a quick-reference or shorthand for the longer name. For example: the assumption "$\delta^{13}C$ offset value between ingested flesh and human collagen in the case of consumption of marine mammals" will sometimes be abbreviated as Assumption #42.

These assumption numbers are listed in Table 1. Note that what is listed as the "Offset" is the fractionation effect between the isotope value of the consumed food and the isotope value for human bone collagen.

## OFFSET VALUES DUE TO FRACTIONATION EFFECTS, TROPHIC LEVEL CHANGES, AND CONVERSION FROM ONE TISSUE TO ANOTHER. ASSUMPTIONS 36-56, AND 61-63

For this present study we have chosen to refer to the differences between the values of ingested tissue and human bone collagen as 'offset values'. This is because these

differences occur for different reasons, depending on which isotope is being considered.

In the case of **Carbon**, there is a difference between a $\delta^{13}C$ value for tissue which an animal (such as a human) consumes and the $\delta^{13}C$ value in the bone collagen of the same animal. This is because the body fractionates carbon during metabolism. Moreover, this fractionation effect is not uniform from one animal tissue to another.

There are therefore two different effects which need to be distinguished in the case of Carbon.

> **$\delta^{13}C$ Offset Value due to Fractionation Effect**: This is defined as the difference between the $\delta^{13}C$ values of food consumed and a tissue in the animal's body. For example, the difference between food consumed by a human and the resulting value in human bone collagen.
>
> **$\delta^{13}C$ Offset Value due to Conversion between Tissues**: In tabulating $\delta^{13}C$ values for animal foods eaten by humans the relevant values are those for the flesh of the animal. Unfortunately, not all published values relate to flesh — some are for bone collagen of the animals concerned. Because there are differences between the $\delta^{13}C$ values for different tissues it is necessary to convert bone collagen values to putative tissue values in these cases. Those animal values in Tables 2 and 3 which have been converted from bone collagen values are identified by an asterisk.

In the case of assimilation of **Nitrogen** into the human body we have not been able to find any documentation on possible fractionation effects between the ingested tissue and the resulting human bone collagen. In the meantime, this fractionation is assumed to be negligible. However, a trophic level effect certainly exists for nitrogen and this must be taken into account. In particular, the $\delta^{15}N$ values become progressively enriched at each trophic level of the food chain (Schoeninger and DeNiro 1984: 632; Schwarcz 1991: 268). Thus, the $\delta^{15}N$ values in human bone collagen are heavier than those of the ingested tissue.

> **$\delta^{15}N$ Offset Value due to Trophic Effects:** This is the difference between the $\delta^{15}N$ values of food consumed and the corresponding value in human bone collagen.

For **Sulphur**, a small trophic level effect appears to exist, with $\delta^{34}S$ values becoming progressively lighter at each higher level of a food chain.

**$\delta^{34}S$ Offset Value due to Trophic Effects:** This is the difference between the $\delta^{34}S$ values of food consumed and the corresponding value in human bone collagen.

**$\delta^{34}S$ Offset Value due to Conversion between Tissues**: As in the case of carbon, it is sometimes necessary to convert values between one tissue type and another for foods consumed by humans.

### $\delta^{13}C$ Offset values from food to human collagen — Assumptions 36-42

It has been reliably established that carbon is fractionated by the body during the assimilation of the isotope, so that the difference between dietary protein and human bone collagen is +5 ± 1‰ (Keegan and DeNiro 1988: 329). There is no evidence to suggest that the extent of fractionation is different for different types of foods eaten, so it is assumed that it is the same for all food types. Therefore, the value of +5‰ will be used as the offset value between all $\delta^{13}C$ food values and $\delta^{13}C$ values for human bone collagen.

Assumptions 36-42: +5.0‰

### $\delta^{15}N$ Offset values from food to human collagen — Assumptions 43-49

A trophic level enrichment in $\delta^{15}N$ values of approximately +3‰ at each level of the food chain has been identified (Schoeninger and DeNiro 1984: 625). This means that a $\delta^{15}N$ value for human bone collagen will be approximately 3‰ more positive than the value of the diet. There is no reason to believe that this enrichment is different for different foods eaten, so it is assumed that the enrichment is the same for all food types. Therefore, the value of +3‰ will be used as the offset value between all $\delta^{15}N$ food values and $\delta^{15}N$ values for human bone collagen.

Assumptions 43-49: +3.0‰

### $\delta^{34}S$ Offset values from food to human collagen — Assumptions 50-56

While the evidence for determining sulphur offset values is limited, and the following discussion may be revised as more information becomes available, it appears that sulphur offset values may be different for marine and terrestrial food chains. Peterson *et al.* (1986: 869) have identified a shift in $\delta^{34}S$ values of -0.5‰ per trophic level of the terrestrial food chain. In contrast, an average trophic level shift of -0.9‰ for marine food chains is likely, as discussed above. Therefore, it seems appropriate to use two offset values for sulphur, one for terrestrial food chains and one for marine. Therefore,

the value of -0.5‰ will be used as the offset value between terrestrial $\delta^{34}S$ food values and $\delta^{34}S$ values for human bone collagen, while the value of -0.9‰ will be used as the offset value between marine food values and bone collagen.

Assumptions 50-52: -0.5‰
Assumptions 53-56: -0.9‰

### $\delta^{13}C$ Offset value due to conversion between tissues — Assumption 61

It has been established that, for carbon, the fractionation between dietary protein and consumer muscle tissue is in the order of +1‰ (Tieszen *et al.* 1983), while between dietary protein and consumer bone collagen the offset is +5 ± 1‰ (Keegan and DeNiro 1988: 329) (the status of this error margin is not described and is therefore unknown). Keegan and DeNiro (ibid.) have defined an isotopic relation of flesh to bone collagen "based on prior reports for terrestrial animals and on measurements of both tissues in 17 modern fishes", whereby the $\delta^{13}C$ flesh values are on average 3.7‰ more negative than those for bone collagen. Keegan and DeNiro's 'fractionation factor', more appropriately termed the conversion factor, of -3.7‰ will be used to convert bone collagen carbon values to flesh values for the tables of assumptions. There is no evidence to suggest that the conversion value between carbon bone collagen values and flesh values will differ according to the foods eaten, therefore it is assumed that the value is the same.

Assumption 61, the difference between the $\delta^{13}C$ value for animal bone collagen and the tissue of the same animal, is taken to be -3.7‰. This value is used to derive some values for Tables 2 and 3, but is not used thereafter in the simulation software.

Assumption 61: -3.7‰

### $\delta^{15}N$ Offset value due to conversion between tissues — Assumption 62

The situation for nitrogen is less clear. Keegan and DeNiro (ibid.) have used a conversion factor of +1.7 ± 0.7‰ (the status of this error margin is not described and is therefore unknown) to convert bone collagen nitrogen isotope ratios to flesh values, based on their findings that $\delta^{15}N$ muscle values are on average 1.7‰ more positive than $\delta^{15}N$ bone collagen values. However, Hobson notes that for nitrogen the difference between dietary protein and consumer muscle tissue appears close to 3-4‰, and also that the difference between dietary protein and consumer bone collagen is between 2.4 and 4‰ (Hobson 1990: 898). This suggests that there may be little difference between nitrogen bone collagen and flesh values. Ambrose (1991: 297) states that "there appears to be no significant average difference in $\delta^{15}N$ values of flesh versus bone collagen of the same mammal".

Because this question appears to be as yet unresolved it has been decided to assume that nitrogen bone collagen values do not differ from nitrogen muscle values, and to include raw nitrogen bone collagen values in the tables of assumptions. There is no reason to believe that there is some difference between nitrogen bone collagen values and flesh values for some foods eaten, therefore it is assumed that the value is zero for all foods.

Assumption 62, the difference between an animal bone collagen nitrogen value and an animal tissue nitrogen value, is taken to be 0.0‰. This value is used to derive some values for Tables 2 and 3, but is not used thereafter in the simulation software.

Assumption 62: 0.0‰

### $\delta^{34}S$ Offset value due to conversion between tissues — Assumption 63

For sulphur no specific data on differences in $\delta^{34}S$ values of flesh and bone collagen could be located. However, evidence of small trophic level shifts in the marine environment can be used to predict a possible difference. Mean values for marine algae, +19.6‰ (Kaplan *et al.* 1963: 313); marine shellfish, +18.8‰ (Mekhtiyeva *et al.* 1976: 85); and marine fish, +17.7‰ from flesh (ibid.) suggest that there may be a shift of around -0.9‰ for each trophic level of the marine food chain. Krouse and Ueda (1987: 118) have also suggested that sulphur values may become progressively lighter at each higher trophic level of the marine food chain. If this is the case, it can be predicted that a $\delta^{34}S$ flesh value from a marine mammal would be in the region of +16.8‰ if the average trophic level shift of -0.9‰ is used in the calculation. This value can be compared with a $\delta^{34}S$ bone collagen value of +16.4‰ for a sea lion from the Auckland Islands (Quinn 1990: 170), and suggests that the difference between sulphur flesh values and bone collagen values may be in the order of 0.4‰. In the absence of any other data for sulphur it has been decided to convert sulphur bone collagen values to flesh values using the conversion factor of +0.4‰. There is no evidence to suggest that the difference between sulphur bone collagen values and flesh values is different for different foods eaten, therefore it is assumed that the value is the same for all foods.

Assumption 63, the difference between an animal bone collagen sulphur value and an animal tissue sulphur value, is taken to be +0.4‰. This value is used to derive some values for Tables 2 and 3, but is not used thereafter in the simulation software.

Assumption 63: +0.4‰

## MEAN $\delta^{13}C$ VALUES FOR PACIFIC FOODS. ASSUMPTIONS 1-7

### $\delta^{13}C$ in C3 plants and tubers — Assumption 1

A range of carbon isotope values has been recorded for modern C3 plants, but there is general agreement that the mean value lies somewhere between -26 and -28‰ (Tieszen 1991: 229), with reported mean values of -26.5‰ (van der Merwe 1982: 599) and -27.1‰ (Tieszen 1991: 229) tending to narrow the range. DeNiro (1987: 183) points out that in prehistoric times, before the industrial revolution, $\delta^{13}C$ values of atmospheric $CO_2$ and consequently both C3 and C4 plants, were more positive by around 1‰ than the values of their modern counterparts. He suggests a value of -26‰ for prehistoric C3 plants which is equivalent to a modern value of -27‰.

Unfortunately, few plant values have been reported for species which are relevant to Pacific diet, but some tuber results are provided in Table 8. These are very similar to those reported for other C3 plants, and the value of -26.0‰ for C3 plants has been selected for inclusion in Tables 1 and 2.

Assumption 1: -26.0‰

### $\delta^{13}C$ in C4 plants — Assumption 2

Similarly, modern C4 plant mean values lie between -12 and -14‰ (Tieszen 1991: 229) with reported mean values lying between -12.5‰ (van der Merwe 1982: 559) and -13.1‰ (Tieszen 1991: 229). DeNiro suggests a prehistoric value for C4 plants of -11.5‰ which is equivalent to a modern value of 12.5‰. A few additional values are given in Table 9. DeNiro's suggested value of -11.5‰ for C4 plants has therefore been assumed for this study.

Assumption 2: -11.5‰

### $\delta^{13}C$ in land herbivores — Assumption 3

Bone collagen $\delta^{13}C$ values for land herbivores range from a mean of -22.23 ± 0.08‰[2], calculated from 10 published deer values from Southern Ontario (Katzenberg 1989:

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[2]Throughout this discussion of assumptions, unless otherwise stated, all nominated error margins of the central tendency of a distribution (the mean) refer to the standard error of the mean. We note that in publications on this subject it is frequently quite unclear what stated error margins refer to, and there is clearly little standardisation in reporting confidence limits. Some comment is therefore in order. In the case of poisson distributions, a statement of confidence limits normally refers to the standard deviation because this is entirely determined by the number of observations ( $\sigma = \sqrt{N}$). As the number of obserobservations increase the confidence limits decrease. However, for parametric distributions the

323) (see Table 4) to a published mean value of -18.9 ± 0.5‰[3] for 21 herbivores (birds and mammals) from a range of locations (Schoeninger and DeNiro 1984: 632). The more positive value is considered to be more representative of terrestrial herbivores in general because it is not derived from one single species or from one environment. This value can be converted to a flesh value, according to Assumption #61, to produce a value of -22.6‰ for land herbivores. This value has been selected for inclusion in the tables.

Assumption 3: -22.6‰

### $\delta^{13}C$ in marine shellfish — Assumption 4

Several $\delta^{13}C$ values for the flesh of marine shellfish have been published (Keegan and DeNiro 1988: 325; Fry *et al.* 1983: 712), ranging between -8.4‰ and -15.6‰ (see Table 5). These include values for a gastropod (*Bittium varium*), a mega-gastropod (*Strombus gigas*) and 13 bivalves collected from inshore reef areas adjacent to shallow grass flats in Torres Strait. A detailed study of the cockle, *Austronvenus stutchburyi*, in an estuarine environment in New Zealand (Stephenson and Lyon 1982) showed that the food sources of this species could be determined from $\delta^{13}C$ flesh values, reflecting the origin of suspended particulate matter in inflowing water on which the animal feeds. Values for $\delta^{13}C$ accordingly varied from -16.7 to -23.5‰. This study is comparable in finding to that of $\delta^{34}S$ in salt marsh plant species (See Assumptions 16a and 16b), published by Peterson *et al.* (1985: 1361;1986: 868).

Given this variability for the New Zealand cockle, it has been excluded from the tabulated results. Unfortunately, this type of problem is likely to affect all three isotopes involved in this study for estuarine species whose primary source of nutrition is suspended particulate material. Likely species in New Zealand include the pipi, *Paphies australe* as well as the cockle.

Lyon (n.d.) has obtained $\delta^{13}C$ results for several other New Zealand species of marine shellfish from the Marlborough Sounds, and these show rather lighter figures than tropical species. He has also carried out an intensive study of 126 specimens of the New Zealand green mussel, *Perna canaliculus*, in the Marlborough Sounds throughout the seasonal cycle. No clear changes were detected from one month to another.

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standard deviation is not a suitable expression of confidence limits of the mean because as the number of observations increase the standard deviation settles down to a fixed value. The standard error of the mean, on the other hand, decreases with increased observations, and therefore constitutes an appropriate measure of the confidence limits of the calculated mean value. This is the reason why it is preferred, except in cases of poisson distributions.

[3] In the original published table the SD is given as 2.3 and N=21. Therefore the SE mean was calculated as ±0.5.

Excluding the cockle, values for all available species are listed in Table 5 from which a mean $\delta^{13}C$ value for marine shellfish of -13.98‰ can be calculated, and this, rounded to one significant figure, -14.0‰, is assumed to be a reasonable value for this assumption.

Assumption 4: -14.0‰

### $\delta^{13}C$ in coral reef fish — Assumption 5

A large number of $\delta^{13}C$ values for reef fish are available. Keegan and DeNiro (1988: 326) have published $\delta^{13}C$ values for muscle from 31 modern reef fish from Grand Bahama Island (see Table 6). From these values they calculated a mean value of -12.59 ± 0.41‰.

Sea grass meadows, like coral reefs, tend to be enriched in $\delta^{13}C$ and fish from both environments tend to have similar $\delta^{13}C$ values. Fry *et al.* (1983: 711) have published the following mean $\delta^{13}C$ values for flesh from a total of 13 fish from sea grass meadows in Torres Straight (see Table 6): -8.4‰ (N=3), -14.1‰ (N=4) and -13.6‰ (N=6) and these figures provide a second mean value of -12.55‰. From all available figures for 44 fish an overall mean of -12.58‰ can be calculated, and this figure is used for the tables of assumptions (rounded to one significant digit -12.6‰).

Assumption 5: -12.6‰

### $\delta^{13}C$ in non-reef marine fish — Assumption 6

Schoeninger and DeNiro (1984: 632) have published values for 10 non-reef fish from which a mean bone collagen $\delta^{13}C$ value of -12.5 ± 0.43‰ can be calculated. This value can be converted to a flesh value of -16.2‰, according to Assumption #61, and can be compared with two mean flesh values of -17.5 ± 1.0‰ (N=3) and -17.9 ± 0.8‰ (N=5) for marine fish from coastal British Columbia (Hobson 1990: 899). Values for nine New Zealand species can be added to this (Lyon n.d.), giving a mean of -16.5 ± 0.7‰ (N=9). An overall mean value of -16.48‰ was calculated from the above values for 21 species (see Table 7) and this value will be rounded to one significant digit as -16.5‰ for use in the tables of assumptions.

Assumption 6: -16.5‰

### $\delta^{13}C$ in marine mammals — Assumption 7

A published mean bone collagen $\delta^{13}C$ value for 41 marine mammals of -13.1 ± 1.6‰ (Schoeninger and DeNiro 1984: 632) can be converted to a flesh value of -16.8‰. This can be compared to a bone collagen value of -13.23‰, equivalent to a flesh value

of -16.93‰, for a sea lion from the Auckland Islands (Quinn 1990: 170). The mean value of -16.80‰, which can be calculated for 42 animals from the above values, is the same as Schoeninger and DeNiro's mean for 41 animals, and this will be used in the tables of assumptions.

Assumption 7: -16.8‰

## MEAN $\delta^{15}N$ VALUES FOR PACIFIC FOODS. ASSUMPTIONS 8-14.

### $\delta^{15}N$ in C3 plants and tubers — Assumption 8

Nitrogen isotope ratios for modern terrestrial plants cover a wide range of values, for example from -2 to +2‰ for legumes (Peterson and Fry 1987: 306) and from -0.4 to +13.5‰ for all plant types from 17 South African collection sites (Ambrose 1991: 297). Ambrose (ibid.: 312) suggests that variations in the $\delta^{15}N$ values of soils, plants and animals can be caused by habitat and climatic variations. It is therefore difficult to select a representative mean value for terrestrial C3 plants. If the range of values from -2 to +13.5‰ is selected, the median value is +5.75‰. This can be compared with a published mean value of +3‰ for all modern terrestrial plants (DeNiro 1987: 187) and a calculated mean value of +4.1 ± 0.58‰ (see Table 8) for cultivated C3 roots and tubers (Keegan and DeNiro 1988).

DeNiro (1987: 184) suggests that prehistoric non-leguminous cultigens had $\delta^{15}N$ values that were more positive than those of their modern counterparts, because of the current widespread use of chemical fertilisers, and that these cultigens may have had $\delta^{15}N$ values that averaged about +9‰. In a subsequent study Keegan and DeNiro (1988: 331) added 3‰ to modern measured $\delta^{15}N$ values for cultigens to obtain $\delta^{15}N$ values for their prehistoric equivalents, thus obtaining a $\delta^{15}N$ value for prehistoric cultivated roots and tubers of +7.0‰.

While this may be an appropriate adjustment to make when reconstructing the diet of a prehistoric group of known horticulturists, for several of the groups in this present study it is unclear whether the plant foods in their diets were cultivated or gathered, and such an adjustment may therefore not be justified. Because a standard representative value must be selected for the tables of assumptions it has been decided to select the median $\delta^{15}N$ value in the published range of values, from -2 to +13.5‰. The median value of +5.75‰ will be used as the value for C3 plants and this will be rounded to one significant digit, giving a value of +5.8‰ for inclusion in the tables of assumptions.

Assumption 8: +5.8‰

### $\delta^{15}N$ in C4 plants — Assumption 9

The available data on C4 plant nitrogen isotope ratios is limited. Only two published values, +10.00‰ for maize (Keegan and DeNiro 1988: 324) and +3.8 ± 0.98‰ for *Spartina*, a C4 marsh plant (Peterson *et al.* 1985: 1361), could be located (See Table 9). In most other studies (for example DeNiro 1987: 184; Ambrose 1991: 297; Sealy *et al.* 1987: 2707) no distinction is made between $\delta^{15}N$ values for C3 and C4 plants, although no specific values are given. The above value for *Spartina* may not be a representative value for terrestrial C4 plants because it is derived from a salt marsh environment. In the absence of other information it has been decided to select Keegan and DeNiro's value of +10.00‰ for maize as the C4 plant value in the tables of assumptions, although further research into $\delta^{15}N$ values for C4 plants may prompt a reinterpretation of this value.

Assumption 9: +10.0‰

### $\delta^{15}N$ in land herbivores — Assumption 10

A wider range of nitrogen values for land herbivores is available (See Table 4), with mean values generally being in agreement. For example Schoeninger and DeNiro (1984: 632) have published a mean value of +5.3 ± 0.41‰ for 21 terrestrial herbivores (birds and mammals) from a variety of locations, while a mean of +5.48 ± 0.19‰ has been calculated (see Table 4) from 9 published deer values from Southern Ontario (Katzenberg 1989: 323). An overall mean of +5.35‰ can be calculated from these two means.

However, the above mean value may not be representative of all land herbivores. Recent research has revealed that terrestrial herbivores living in areas of low rainfall, 400 mm per year, have higher $\delta^{15}N$ values, > +10‰, due to water conserving metabolic processes within the animals (Sealy *et al.* 1987: 2713). For the purposes of this present study this problem may not be relevant because prehistoric populations living on Pacific Islands generally did not have access to wild terrestrial herbivores, although birds were included in their diets. It is not known, however, whether birds have the same water conserving metabolism that has been found in some large African animals such as elands and wart-hogs (ibid.). For groups like the inland Nebira people of Papua New Guinea, who lived in areas where larger herbivores were available, there is almost certainly no need to allow for higher nitrogen values for these animals. Although the Port Moresby area, in which Nebira is located, tends to have a seasonal climate with some dry months, the annual rainfall is in the range of 780–1520 mm (Bulmer 1978: 16). A $\delta^{15}N$ value of +5.59‰ for a wallaby from Motupore (Quinn 1990: 170), a small offshore island about 16 km to the east of Port Moresby, tends to confirm that terrestrial herbivores from this area do not have elevated $\delta^{15}N$ values.

Therefore it has been decided to include the calculated overall mean of +5.35‰, rounded to one significant digit, giving a value of +5.4‰ for this assumption.

Assumption 10: +5.4‰

### $\delta^{15}N$ in marine shellfish — Assumption 11

A range of nitrogen values for marine shellfish has been published, from a variety of locations. Two values from Providenciales in the Turks and Caicos Islands (Keegan and DeNiro 1988: 325) for a gastropod and a mega-gastropod, give a calculated mean value of +2.9 ± 0.8‰ (see Table 5). A group of nine values for marine shellfish from South Africa's South-western Cape (Sealy *et al.* 1987: 2709) give a calculated mean value of +8.11 ± 0.2‰(see Table 5). This group comprises five filter feeders (*Choromytilus* sp.) and four grazers and detritus feeders (*Patella* sp. and *Haliotis* sp.) (ibid.). Because the groups of people in this present study are likely to have eaten a wide range of shellfish it is considered appropriate to calculate a mean value from all 11 available nitrogen values. This is the approach taken in Table 5, and provides a mean value of +7.16 ± 0.67‰. This value is rounded to +7.2‰ as a suitable figure for marine shellfish.

Assumption 11: +7.2‰

### $\delta^{15}N$ in coral reef fish — Assumption 12

In recent years extensive research into nitrogen values from coral reef environments (for example, Schoeninger and DeNiro 1984; Keegan and DeNiro 1988) has revealed that nitrogen values for reef fish are consistently lower than open ocean marine values, because of the increased amount of nitrogen fixation by blue-green algae in coral reef areas (DeNiro 1987: 189). A range of reliable published values is available for reef fish. One mean value of +5.5‰ for four reef fish has been published by Schoeninger and DeNiro (1984: 632), and values for 31 reef fish from the Bahamas are given by Keegan and DeNiro (1988: 326). The latter are listed in Table 6, and were used to calculate a mean of +7.85 ± 0.18‰. The mean is rounded to one significant digit to give a value of +7.9‰ for this assumption.

Assumption 12: +7.9‰

### $\delta^{15}N$ in non-reef marine fish — Assumption 13

As discussed above, nitrogen values for non-reef fish tend to be higher than those for reef fish. A mean value of +13.8 ± 0.51‰ for the first 10 values listed in Table 7 is derived from values published for marine fish by Schoeninger and DeNiro (1984: 632). This can be compared with a published mean value of +14.3 ± 0.3‰ for five marine

fish (*Ammodtyes* sp.) from coastal British Columbia (Hobson 1990: 899). The full set of data produces a mean of +13.94‰ (see Table 7) and is rounded to one significant digit, giving a value of +14.0‰ which will be included in the tables of assumptions.

Assumption 13: +14.0‰

### $\delta^{15}N$ in marine mammals — Assumption 14

Marine mammals tend to have nitrogen values which are 2-3‰ higher than those of marine fish, which reflects their higher position in the marine food chain. A difference of 3‰ has been observed between different trophic levels of food chains (Schoeninger and DeNiro 1984: 632), so that animals which occupy lower positions in a food chain have lower nitrogen values. A mean value of +15.6 ± 0.34‰ for 41 marine mammals (Schoeninger and DeNiro 1984: 632) can be compared with two values for cape fur seals from South Africa of +15.9‰ and +19.3‰ (Sealy *et al.* 1987: 2709), and a value of +18.13‰ for a sea lion from the Auckland Islands (Quinn 1990: 170). An overall mean of +15.74‰ can be calculated from these values and this will be used in the tables of assumptions, after rounding to one significant digit, to give a value of +15.7‰.

Assumption 14: +15.7‰

## MEAN $\delta^{34}S$ VALUES FOR PACIFIC FOODS. ASSUMPTIONS 15-21

As discussed above, the selection of suitable sulphur values for the tables of assumptions is complicated by the fact that soils which derive from marine sediments, and consequently the plants that grow in these soils and the animals or people feeding on those plants, have sulphur values close to marine sulphate, which has a value between +20 and +21‰ (Peterson and Fry 1987: 303; Kaplan *et al.* 1963: 312). Kusakabe *et al.* (1976: 436) found that most soluble and adsorbed soil sulphates in New Zealand soils have values close to those of present-day seawater, or to those of evaporates of marine sulphate, that is +17‰ (Kusakabe *et al.* 1976: 436), which suggested to them "that sea spray or precipitation high in marine sulphate is the principal source of sulphur" in these areas (Kusakabe *et al.* 1976: 436). It is therefore likely that plants growing close to the sea will obtain most of their sulphur from the marine environment, irrespective of whether the soil is derived from marine sediments. They also suggest that soils containing volcanic materials would have lower sulphur values as volcanic material tends to be lighter than marine sulphate, although volcanic sulphur in New Zealand can sometimes exceed +20‰ (Kusakabe *et al.* 1976: 436). Clearly then, the sulphur values of terrestrial plants will be determined by the environment and this must be taken into account when selecting values for the tables of assumptions. The following discussion will therefore be concerned with selecting both marine dominated

assumptions (see Table 2) and land dominated assumptions (see Table 3) for the three terrestrial food types — C3 plants, C4 plants and land herbivores. It should be noted here that only a small number of $\delta^{34}S$ values have been published, and consequently Assumptions 15-21 are likely to be revised in future as more $\delta^{34}S$ values become available.

### $\delta^{34}S$ in C3 plants and tubers — Assumption 15a (Marine Dominated)

Plants growing in areas dominated by marine sulphates have been found to have marine-looking sulphur values. Kusakabe *et al.* (1976: 436) have published six sulphur values from New Zealand coastal areas which are more marine-looking than would be expected for terrestrial plants (see Table 8), with a mean value of +15.28 ± 0.84‰. Values for $\delta^{34}S$ of up to +17.1‰ have been obtained for Pacific cultigens such as taro (*Colocasia* sp.) and yam (*Dioscorea* sp.) (see Table 8), which suggests that $\delta^{34}S$ values of C3 plants from marine dominated environments can resemble those of evaporates of marine sulphate, that is +17‰ (Kusakabe *et al.* 1976: 436). A value of +17‰ will thus be included in Table 2 as Assumption 15a, the $\delta^{34}S$ value for C3 plants from a marine dominated environment.

Assumption 15a: +17.0‰

### $\delta^{34}S$ in C3 plants and tubers — Assumption 15b (Land Dominated)

Peterson *et al.* (1985: 1361) have published a mean $\delta^{34}S$ value (N=2) for inland C3 plants of +4.7 ± 0.9‰ (the status of this error margin is not described and is therefore unknown), a value which reflects the sulphate they obtain from precipitation which has a $\delta^{34}S$ value in the range of +2 to +8‰ (Peterson *et al.* 1986: 867). A value for oak leaves from Cape Cod forests of +5.4‰ (ibid.: 869) and observed average values between +2 and +6‰ for continental vegetation (Peterson and Fry 1987: 304) indicate that the above mean for inland plants is reliable. An unweighted mean of +4.93‰ can be calculated from the two values of Peterson *et al.* mentioned above and this mean, rounded to one significant digit +4.9‰, will be included in Table 3 as Assumption 15b, the $\delta^{34}S$ value for C3 plants from land dominated environments.

Assumption 15b: +4.9‰

### $\delta^{34}S$ in C4 plants — Assumption 16a (Marine Dominated)

There is very little information available on the $\delta^{34}S$ values of C4 plants and it is as yet unclear whether sulphur values of C4 and C3 plants from the same environment would be different. Three mean values from a total of 33 samples of *Spartina alterniflora*, a C4 marsh plant, have been published by Peterson *et al.* (1985: 1361;

1986: 868), (see Table 9) and from these an unweighted mean of -3.04‰ can be calculated. The low sulphur values of these samples, which were taken from salt marshes and creek-bank sites, can be explained by the fact that marsh plants rooted in anoxic sediments produce their organic sulphur compounds from pore water sulfides which are greatly depleted in $\delta^{34}S$, relative to sulphate in the pore waters or in seawater (Peterson *et al.* 1986: 868). This suggests that such low $\delta^{34}S$ values may be peculiar to marsh or creek-bank sites and may not apply to C4 plants growing in other marine dominated environments. One other C4 plant sulphur value, +9.8‰ for sugar cane (*Saccharum officinarum*) (see Table 9), seems to be intermediate between the marine dominated and the land dominated values which have been selected above for C3 plants. Because the origin of the sugar cane sample is unknown, it is not possible to determine whether this value reflects the environment in which the sample grew, or whether it reflects the C4 photosynthetic pathway of the sugar cane. It is thus not possible at present to say whether a $\delta^{34}S$ value for a C4 plant from a marine dominated environment would differ from a value for a C3 plant from that same environment. Therefore, Assumption 16a in Table 2 will be taken to be the same as Assumption 15a for C3 plants which is +17‰.

Assumption 16a: +17.0‰

### $\delta^{34}S$ in C4 plants — Assumption 16b (Land Dominated)

From the above discussion it is obvious that it is also not yet possible to determine whether C4 and C3 plants in land dominated environments will have different $\delta^{34}S$ values. Therefore, Assumption 16b, the value for C4 plants from land dominated environments, will be taken to be the same as Assumption 15b for C3 plants, which is +4.9‰.

Assumption 16b: +4.9‰

### $\delta^{34}S$ in land herbivores — Assumption 17a (Marine Dominated)

Only one $\delta^{34}S$ value for a land herbivore could be located. Peterson *et al.* (1986: 869) obtained a $\delta^{34}S$ value of +4.9‰ from a grey squirrel (*Scurus carolinensis*) which had inhabited a Cape Cod forest. A sample of oak leaves from the same location gave a $\delta^{34}S$ value of +5.4‰ which indicated that there was a shift in $\delta^{34}S$ values of -0.5‰ per trophic level (ibid.). For the purposes of the present study this identified trophic level shift will be used to predict a $\delta^{34}S$ value for herbivores eating plants from marine dominated environments. Thus, based on the $\delta^{34}S$ plant values selected for Table 2, +17.0‰ for both C3 and C4 plants, it can be calculated that herbivores eating such

plants would have $\delta^{34}S$ values of +16.5‰. This value will be included in Table 2 as Assumption 17a.

Assumption 17a: +16.5‰

### $\delta^{34}S$ in land herbivores — Assumption 17b (Land Dominated)

Land herbivores eating plants from land dominated environments can also be expected to have $\delta^{34}S$ values which are 0.5‰ lighter than those of the plants on which they feed. Assumption 17b, for inclusion in Table 3, can therefore be calculated to be +4.4‰.

Assumption 17b: +4.4‰

### $\delta^{34}S$ in marine shellfish — Assumption 18

A small number of published $\delta^{34}S$ values for marine shellfish is available (see Table 5) ranging from +16.8‰ for a blue mussel (*Mytilus edulis*) from Woods Hole, Massachusetts (Peterson *et al.* 1986: 869) to +20.9‰ for a black abalone (*Haliotis cracherodii*) from the Gulf of California (Kaplan *et al.* 1963: 330). The calculated mean value of +18.56 ± 0.68‰, rounded to one significant digit, +18.6‰, will be included in Tables 2 and 3 as Assumption 18, the $\delta^{34}S$ value for marine shellfish.

Assumption 18: +18.6‰

### $\delta^{34}S$ in coral reef fish — Assumption 19

No $\delta^{34}S$ values for coral reef fish could be located. However, two low values from Papua New Guinea for a dugong (*Dugong dugon*) of +9.8‰ and a turtle (probably *Chelonia mydas*) of +13.0‰ (Quinn 1990: 170), both animals which are known to feed in sea grass meadows and coral reef areas, suggest that such environments may be depleted in $\delta^{34}S$. Therefore it could be assumed that fish feeding in reef areas may also have lighter sulphur values than would be expected for marine animals. However, the extent to which sulphur values would be reduced in such fish is not known. Until this can be established, it is considered preferable to assume that reef fish have similar $\delta^{34}S$ values to non-reef fish, and therefore the value of +17.7‰, as discussed below, will be selected as Assumption 19 for inclusion in Tables 2 and 3.

Assumption 19: +17.7‰

### $\delta^{34}S$ in non-reef marine fish — Assumption 20

From the available $\delta^{34}S$ values for non-reef fish (see Table 7), which range from +16.9‰ for a haddock (*Melanogrammus aeglefinus*) from the White Sea (Mekhtiyeva

*et al.* 1976: 85) to +18.2‰ for a swordfish (*Xiphias gladius*) from Georges Bank near Cape Cod (Peterson *et al.* 1986: 869), a mean of +17.73 ± 0.29‰ can be calculated. This mean, rounded to one significant digit, +17.7‰, will be included in Tables 2 and 3 as Assumption 20.

Assumption 20: +17.7‰

### $\delta^{34}S$ in marine mammals — Assumption 21

The only available $\delta^{34}S$ value for a marine mammal is a bone collagen value of +16.4‰ for a sea lion (*Phocarctus hookeri*) from the Auckland Islands (Quinn 1990: 170). This can be converted to a flesh value, according to Assumption 63, of +16.8‰ and this will be included in Tables 2 and 3 as Assumption 21.

Assumption 21: +16.8‰

## NUTRITIONAL VALUES OF PACIFIC FOODS. Assumptions 22-35

Various texts were examined for information about nutritional values of foods relevant to prehistoric Pacific populations. This is nowhere near as definitive as it could be; however, some of the available data is summarised in Table 10. This includes plant and animal foods from both the tropical and temperate parts of the Pacific.

### Protein and energy content — Assumptions 22–28 and 29–35

In cases where information was available for a sizeable number of foods in any one category, the mean value was calculated and employed in the simulations (Tables 2 and 3). However, reliable information on reef-fishes is very hard to obtain, and it was considered advisable in the meantime to use the mean value for non-reef fishes.

Values for C4 plants are few, and that available for sugar cane was used (protein 0.4 g/100g and energy 38 kcal/100g). Information is scarce for land herbivores, and the values for chicken were used (protein 23.1 g/100g and energy 155 kcal/100g). Finally, in the case of sea mammals, the values for southern fur seal were used (protein 14.0 g/100g and energy 262 kcal/100g)

| | |
|---|---|
| Assumption 22: | 2.2 g/100g |
| Assumption 23: | 0.4 g/100g |
| Assumption 24: | 23.1 g/100g |
| Assumption 25: | 12.9 g/100g |
| Assumption 26: | 19.7 g/100g |
| Assumption 27: | 19.7 g/100g |
| Assumption 28: | 14.0 g/100g |

| | | |
|---|---|---|
| Assumption 29: | 145 | kcal/100g |
| Assumption 30: | 38 | kcal/100g |
| Assumption 31: | 155 | kcal/100g |
| Assumption 32: | 69 | kcal/100g |
| Assumption 33: | 100 | kcal/100g |
| Assumption 34: | 100 | kcal/100g |
| Assumption 35: | 262 | kcal/100g |

**Range of acceptable daily protein and energy intake — Assumptions 57-60**

| | | |
|---|---|---|
| Assumption 57: | 1800 | kcal/day |
| Assumption 58: | 3700 | kcal/day |
| Assumption 59: | 25 | g/day |
| Assumption 60: | 200 | g/day |

Before an evaluation can be made of the nutritional quality of particular diets or food items, it is necessary to identify the range of acceptable daily protein and energy intakes for the populations being studied. For the purposes of computer simulation, only one value can be included for each of four variables: minimum and maximum daily protein intakes and minimum and maximum daily energy intakes. These values should therefore reflect the nutritional requirements of an average, or representative member of a population, but will be difficult to define as protein and energy requirements can vary considerably, according to factors such as body weight, the physical activity profile, physiological differences and the age and sex of the individual (Beaton 1988: 650). However, it has been established that the main determinants of requirements for both energy and protein are body weight and age, while physical activity is an important determinant for energy requirements (Anon. 1985: 29). In addition, protein requirements are dependent on energy intake and expenditure, and on the quality of the protein consumed (Munro 1985). Finally, after adjusting for all measurable variables, a 12% to 15% variation of nutrient requirement has been measured among individuals (Beaton 1988: 650).

### *A representative individual*

Considering the number of factors which interact to determine an individual's protein and energy requirements, it is clear that in order for any computer simulations to produce meaningful results the physical characteristics of the representative member of the population must be clearly defined. For this present study, in which the diets of prehistoric Pacific populations are being constructed, the most appropriate measures of body weight and height can be found in Sir Peter Buck's anthropometry on the New

Zealand Māori Battalion returning from the First World War (Buck, 1922-23). This group of men included 424 full-blooded Māori from which mean figures were obtained for height of 1706 mm and for weight, 163.9 lbs or 74.34 kg. Buck's study which defined a relatively tall and robust group of New Zealanders can be compared with several early European comments on Māori stature and studies of other Polynesian populations which were considered by Houghton *et al.* (1975). Heights for modern Polynesian males ranged from 1703 mm for Marquesans to 1730 mm for Tongans (Houghton *et al.*: 1975), suggesting that the people were tall throughout Polynesia and that Buck's figures can be considered representative of Polynesian populations.

As discussed above, for the purposes of determining daily nutritional requirements the main criteria which must be considered are weight, age and physical activity. It is difficult to define a value for a mean weight for a population of males and females in prehistory because there is very little weight and stature data available for groups leading a traditional lifestyle in terms of diet, especially female data. A study has recently been made by Houghton (1992: pers. comm.) using a technique developed on radiographs of joints (Behnke, 1959). He estimated the weights of a New Zealand-wide sample of prehistoric skeletons from a series of skeletal measurements. The estimated mean weight for males was 75.5 kg, which compares well with Buck's mean measured weight of 74.34 kg for Māori males. For females the estimated mean weight was 57.5 kg, and while this cannot be compared with any actual measured weights, these estimated figures are in line with the weight ratio of 4: 3 for males and females reported by Behnke (1959: 313). Based on these estimated figures for males and females, a population mean of 66.5 kg can be estimated, assuming that the proportions of males and females in prehistoric New Zealand populations were approximately equal. However, Houghton (ibid.) has suggested that early accounts refer to females in tropical Polynesia as being more robust than their New Zealand counterparts. Because of these observations it has been decided for this present study to choose a slightly more generous population mean weight of 70 kg as being representative of Pacific populations in general. This same figure is frequently used by WHO for calculating acceptable daily intake levels of toxins (WHO, 1976: 22, 78, 80).

The determination of an appropriate age for this representative individual is more straightforward. An adult is considered more appropriate as a population representative because although protein and energy requirements differ according to age within human populations, requirement for nutrients in children is related more to body weight than to age (Anon. 1985: 130). Children and adolescents of both sexes require more nutrients than adults in proportion to their body weights (Anon. 1985: 130 ff.), but adults are generally heavier and thus consumption of nutrients on a population basis would even out. In New Zealand prehistory, and in prehistoric societies generally, the average age at death for adults was around 30 years (see Houghton 1975: 232,

Houghton 1980: 97, Brewis, 1988: 73), so a representative adult could be expected to be in the early twenties.

Daily energy requirements are closely linked to energy expenditure (Beaton 1985: 223). In prehistory the populations of New Zealand and the Pacific relied heavily on the sea for subsistence, and many of these people were also horticulturists. Both of these economic strategies require regular moderate physical activity, similar to the energy expenditure levels attributed to modern subsistence farmers (Anon. 1985: 77).

The individual who is considered representative of a prehistoric Pacific population, for the purposes of determining daily protein and energy intakes, weighs 70 kg, is in the early 20s and engages in daily moderate physical activity.

### *Range of acceptable daily energy intakes*

Recommended energy requirements for human populations generally relate to the maintenance of health in already healthy individuals, so that the level of energy intake from food will balance energy expenditure when the individual has a body size and composition, and level of physical activity, consistent with long-term good health (Anon. 1985: 12). It is thought that there may be physiological risks associated with intakes either above or below actual requirements (ibid.) so it is important to define the range of acceptable intake values within which long-term good health will be maintained.

Recommended values vary according to sex, body weight and activity levels. The South Pacific Commission (Anon. 1983: 32) recommend an energy intake of 3000 kcal/day for a 65 kg moderately active adult man, while a daily intake of 2500 kcal for Asian males is recommended by Wilson (1975). The World Health Organisation's daily average energy requirements for a 70 kg individual range from 2150 kcal for a woman with a low activity level to 3850 kcal for a man with a high level of activity (Anon. 1985: Tables 42 & 45). For moderate activity levels the suggested daily intakes are 2750 kcal for women and 3150 kcal for men (ibid.). These values can be compared with estimated values of energy intakes of actual populations. Hasunen and Pekkarinen studied the diets of two Finnish Lapp populations and reported mean daily energy intakes for one population of 3800 kcal for males and 2620 kcal for females (Draper 1980). This diet was reported as being nutritionally "generally adequate", while the second group which had daily energy intakes as low as 1653 kcal for females had a nutritionally inadequate diet (ibid.). Robson and Wadsworth (1977) cite estimates of the daily energy intake in July for the !Kung of 2140 kcal and 2260 kcal respectively. These figures are low and it has been suggested that at the end of the dry season individuals living on 2260 kcal a day would probably be in negative energy balance (ibid.: 189). Even lower daily energy intakes of 1300-2400 kcal are reported for Papua New Guinea but these values may not be entirely reliable because of lack of knowledge

about actual food intakes (Robson and Wadsworth 1977: 191). Clearly it is possible for people to exist on a fairly broad range of caloric intakes, but it is not yet clear whether health could be maintained if the imbalance between recommended daily intakes and actual intakes continues over long periods of time, to the extent that changes in body weight and composition result (Anon. 1985: 13). The consequences of reduced energy intake will also depend upon the level of pre-existing energy reserves combined with environmental conditions (Beaton 1985: 228).

The definition of an acceptable range of energy intakes is thus not straightforward, considering the number of factors, both environmental and physiological, which can influence the long-term maintenance of good health, in the face of variable energy intakes. It should also be recognised that in prehistory dietary quality and variety may have been limited, particularly in the more temperate areas of Polynesia, so that a diet considered nutritionally inadequate today may have been adequate for at least short-term survival in prehistory. It is therefore considered appropriate to suggest a minimum acceptable daily energy intake level which is lower than recommended levels for modern populations. A figure of 1800 kcal has been selected, based on the World Health Organisation's daily average energy requirement of 2150 kcal for a 70 kg woman with a low activity level, less approximately 15% which is equivalent to the variation of nutrient requirement among individuals (Beaton 1988: 650). A maximum acceptable daily energy intake level should be similar to modern intakes as these reflect the maximum level of nutrients an individual of given body size and activity level can physiologically cope with. A figure of 3700 kcal has been selected, based on the World Health Organisation's daily average energy requirement of 3150 kcal for a 70 kg man with a moderate activity level, plus approximately 15% for variation among individuals (ibid.).

| | |
|---|---|
| Assumption 57: | 1800 kcal/day |
| Assumption 58: | 3700 kcal/day |

### *Range of acceptable daily protein intakes*

Protein requirements depend upon the level of energy intake and upon the quality of protein ingested, with low energy diets generally requiring more protein in order to maintain nitrogen equilibrium and thus preserve tissue protein (Munro 1985: 163). Conversely, if a high-protein diet is consumed, energy requirements may have to be raised by up to 30% because the body's metabolic rate must increase in order to process the digested protein (Speth and Spielmann 1983: 5-6; Noli and Avery 1988: 396). This is referred to as the 'specific dynamic action' or SDA. However, it has been found that there is an upper limit to the total amount of protein which can be consumed on a regular basis. This limit is reached when approximately 50% of total calories are derived from protein (Noli and Avery 1988: 396), but most peoples limit their intake

of protein to around 10-15% of energy needs (Noli and Avery 1988: 396). In fact the ingestion of levels of protein, as low as 23% of energy intake over 10 days, has been observed to cause azotaemia (excess nitrogen) and a rise in plasma ammonia concentration which can be lethal (Noli and Avery 1988: 397). The protein contents of some traditional Eskimo diets have been estimated to be up to 45% of total calories, with a similar proportion of energy needs being derived from fats (Speth 1990: 155). Draper (1980: 259) cites values compiled in 1972 by Bang, Dyerberg and Hjorne for the percentage sources of calories in diets from the coastal Eskimo settlement of Igdlorssuit in northwest Greenland. These were 26.2%, 37.1% and 36.7% for protein, fat and carbohydrate respectively. This data can be compared with records from northwest Greenland made in 1914 which indicated that at that time protein provided 44% of diet calories, fat 47% and carbohydrate 8%. The latter figures reflect a diet with a fat content which could potentially lead to ketonuria, or the accumulation of acidic ketone bodies in the bloodstream from the metabolism of fat, leading to serious illness and death (Anderson 1981: 152, Denniston 1972). It has been suggested that ketonuria can be avoided if carbohydrates comprise at least 15% of the daily diet (Anderson 1981: 153, Davidson *et al.* 1972: 214-216).

Taking the above discussion into consideration, it is possible to define a range of acceptable daily protein intakes within which individuals could be expected to remain healthy. Recommended safe levels of protein intake are generally expressed as grams of protein per kg of body weight, and may vary according to the quality of the protein being consumed (Anon. 1985: 157). These recommended intakes are normally set at the average need plus 2 standard deviations, with a safe consumption level considered to be at or above the `recommended' intake (Beaton 1988: 658). The World Health Organisation (Anon. 1985: 82) sets a protein intake level of 0.75 g/kg/day as sufficient to meet the needs of all but 2.5% of individuals within a population, and this value is thought to correspond with the lower end of the safe range of protein intakes. This converts to a daily intake of 52.5 g of protein for our representative individual weighing 70 kg. Beaton (1988: 652) calculates a recommended daily protein intake of 57 g for a 25 year old, 70 kg adult male, based on a recommended intake of 0.81 g/kg, and suggests that a daily protein intake of 25 g or lower would be 100% inadequate for a randomly selected individual. However, daily protein intakes varying between 10 and 40 g have been reported for populations in Papua New Guinea, although the reliability of these values has been questioned (Robson and Wadsworth 1977: 191). This does suggest though that low levels of protein intake may be acceptable for a period of time. To some extent the human body may be able to adjust to lower protein intakes by reducing protein breakdown (Young *et al.* 1985: 199), but ultimately a long-term very low protein diet leads to stunting and nutritional dwarfism (Golden 1985: 174). One other point should be considered here. The lower limits of acceptable protein intakes can vary between individuals, with the coefficient of individual variability of protein requirement per kg of body weight being estimated as approximately 12.5% (Beaton

1985: 221). For the computer simulation it is thus considered reasonable to select a value of 25g per day as the lowest possible acceptable protein intake.

The upper limits of protein intakes can be considerably higher than the recommended daily allowances, as the human body is able to adjust absorption, excretion and catabolism for some nutrients, in a way which serves to maintain health over a range of intakes (Beaton 1985: 220). An extreme upper limit to the amount of protein that can be consumed safely on a sustained basis, approximately 300 g per day, has been proposed by Speth (1990: 155). This figure represents a protein intake of roughly 50% of total per capita daily caloric intake under normal, non-stressful conditions (ibid.). As discussed above, a more realistic maximum daily protein intake may represent 20-30% of daily caloric intake, and would be in the region of 120-180 g of protein per day. Draper (1977: 311) has reported a protein intake of 200 g per day for pre-modern Arctic Eskimo, an intake which represented 32% of their daily caloric intake. This figure will be taken as the maximum acceptable daily protein intake.

| | | |
|---|---|---|
| Assumption 59: | 25 | g/day |
| Assumption 60: | 200 | g/day |

## DESCRIPTION OF THE ALGORITHM

The computer simulation software was written by Leach in Turbo Pascal 5, and runs in a PC environment. It incorporates only a modest amount of graphics, designed to allow the user to evaluate how quickly successful simulations are discovered. If the rate is very low, then the user can stop the software and change the operating conditions, for example, by widening various tolerance levels. It was found that a 20 MHz 386 environment is reasonably satisfactory, but that a typical run was 24 hours or more. The software in a pentium environment running at 90 MHz was far more satisfactory. The software flow chart is relatively straightforward, and has twelve discrete steps:

Step 1: Read all the assumptions being used for a particular problem. This consists of the values presented in either Table 2 or Table 3 plus the mean isotope signature for the group of people being studied, together with any known food proportions, established from archaeological studies.

Step 2: Choose one of three modes of operation.
Mode 1 presents running statistical data on valid simulations relating to food values and isotopes.
Mode 2 graphically displays running histograms of food weight percentages.
Mode 3 graphically displays bar charts of running mean and standard deviation for each food type.

Step 3: Randomly generate food percentages by weight for each food type. These must be within the range specified at Step 1. The random generator used is a flat one across a stated distribution, although it does not have to be this type. We could also use a normalised distribution with a pre-defined SD. This would tend to generate more values around the stated central point, and therefore produce a greater rate of valid simulations. However, there would be a certain amount of circular argument in this approach, whereby valid simulations are loaded towards the centre of expectations. Although the flat distribution technique is much slower, producing numerous unlikely or impossible combinations, it is probably wiser because any unexpected food combinations which produce the prehistoric isotope signature will be found. The most conservative approach is to generate a flat distribution from 0 to 100% (coding 50 as the central value with a margin value of 50). In cases where there is good faunal analysis data for the prehistoric community being studied, the simulation will speed up if some reasonable limits are indicated from this data.

In cases where it is known that a certain food type simply does not exist in the economy involved, such as no C4 plants, or no coral reef, then a value of 0 and 0 can be used. In this way, any simulations containing these food types will be rejected.

Step 4: Randomly generate a value of total energy for all foods in kcals within the margins stated at Step 1.

Step 5: From the information in Steps 3 and 4, calculate the weight composition for each food type.

Step 6: Using the weight data in Step 5 and the assumptions in Step 1, calculate the energy values for this weight of each food.

Step 7: Using the weight data in Step 5 and the assumptions in Step 1, calculate the amount of protein for this weight of each food.

Step 8: Check whether the total protein calculated in Step 7 is within acceptable boundaries, specified in Step 1. If it is not acceptable, go back to Step 3 and start the simulation again, otherwise go to Step 9.

Step 9: Calculate the isotope signature in collagen which a person consuming the simulated diet would have.

Step 10: Check whether this isotope signature falls within the range stipulated for this prehistoric group in Step 1. If it is not acceptable, go back to Step 3 and start the simulation again, otherwise go to Step 11.

Step 11: Check whether the calculated weight data for each food falls within the ranges specified from known archaeological data in Step 1. If it is not acceptable, go back to Step 3 and start the simulation again, otherwise go to Step 12.

Step 12: **This is a valid simulation.** Accumulate running statistics, such as food weight percentages, energy and protein values for each food, minimum and maximum values. Carry out various computer housekeeping processes relating to the mode of operation. Finally, return to Step 3 and start the simulation process again, until interrupted by the user.

## THE REVERSE EXPERIMENT

It is possible to run the simulation software backwards—that is, specify a theoretical food weight composition, forward calculate the collagen isotope values which would result from eating such a diet, and then run the software to check that the theoretical diet can be reproduced. This is a useful test of how reliably one can work backwards from isotope signatures in reconstructing prehistoric diets. This was attempted as follows:

For the purposes of this experiment, a theoretical diet was pre-defined with the following weight composition:

| | |
|---|---|
| 1 = C3 Plants | 20% |
| 2 = C4 Plants | 5% |
| 3 = Land Herbivores | 4% |
| 4 = Marine Shellfish | 3% |
| 5 = Coral Reef Fish | 13% |
| 6 = Non-Reef Fish | 10% |
| 7 = Marine Mammals | 45% |

Using the appropriate assumptions, this diet should produce a unique isotope signature of:

| | |
|---|---|
| $\delta^{13}C$ | -18.4‰ |
| $\delta^{15}N$ | +12.9‰ |
| $\delta^{34}S$ | +13.3‰ |

The software was then run using this hypothetical isotope signature and the same assumptions used to see what kind of food composition would be reconstructed, as a

test of how close it would be to the pre-defined theoretical diet. A total of 143 valid simulations were found for 3,857,711 trials. This low rate was partly because a close tolerance of ± 0.5‰ was specified for each isotope. The valid simulations resulted in the following values:

| | Mean | SD |
|---|---|---|
| $\delta^{13}C$ | -18.4 | 0.3 |
| $\delta^{15}N$ | +12.7 | 0.2 |
| $\delta^{34}S$ | +13.4 | 0.3 |
| kcal | 1673 | 191 |
| protein g | 129 | 14 |

| **Food** | **Target %** | **Mean %** | **SD %** | **Difference %** |
|---|---|---|---|---|
| 1 = C3 Plants | 20 | 15.2 | 6.8 | 4.8 |
| 2 = C4 Plants | 5 | 5.1 | 2.1 | 0.1 |
| 3 = Land Herbivores | 4 | 8.5 | 6.5 | 4.5 |
| 4 = Marine Shellfish | 3 | 4.8 | 3.7 | 1.8 |
| 5 = Coral Reef Fish | 13 | 11.5 | 8.1 | 1.5 |
| 6 = Non-Reef Fish | 10 | 11.3 | 7.4 | 1.3 |
| 7 = Marine Mammals | 45 | 43.6 | 4.8 | 1.4 |

This 'Reverse Experiment' produced mean food weight ranges which contain the target figures. The rather high standard deviations result from the relatively small number of valid simulations. This test gives considerable confidence in the method.

## APPLICATION OF THE ALGORITHM

We have been investigating the isotope composition of human bone samples from a number of parts of the Pacific in conjunction with a wider programme of research on prehistoric diet in the Pacific. We have applied the algorithm to two prehistoric groups — one which lived on the Island of Watom near New Britain (Leach *et al.* in press), and the other which lived in the Chatham Islands near New Zealand. The latter study is used here to describe the algorithm in action mainly because there is quality information available from classical midden analysis of some aspects of the diet, notably of meat foods. The details of the isotope and midden analysis results for this prehistoric community are given elsewhere (Leach *et al.* n.d.), and only a summary is provided here.

Detailed analysis of bone and shell middens on the island suggest that the approximate proportions of food types by weight were as follows:

| | | |
|---|---|---|
| C3 Plants | ? | No information from midden analysis |
| C4 Plants | 0% | No edible species present on island |
| Land Herbivores (birds) | 4% | |
| Marine Shellfish | 4% | |
| Coral Reef Fish | 0% | Not present on island |
| Non-Reef Fish | 24% | |
| Marine Mammals | 68% | |

The cumulative percentage is 100% in this reconstruction, and obviously needs adjusting downwards to take into account the presently unknown contribution from plant foods. In setting up a series of assumptions for the isotope model for this community, some 'slop' should be permitted in these proportions. The width of the filters were chosen as ± 5% for both Land Herbivores and Marine Shellfish, and ± 10% for both Marine Fish and Sea Mammals. Simulations were permitted in a wide range around these central values derived from midden analysis, but only solutions falling within these stated margins were retained for later examination.

Thus, this part of the simulation conditions can be summarised as follows:

| **Food Type** | **Archaeological** | **Filter** | **Simulation Range** |
|---|---|---|---|
| C3 Plants | ? | None | 50% ± 50% |
| C4 Plants | 0% | None | 0% ± 0% |
| Land Herbivores (birds) | 4% | ± 5% | 20% ± 20% |
| Marine Shellfish | 4% | ± 5% | 20% ± 20% |
| Coral Reef Fish | 0% | None | 0% ± 0% |
| Non-Reef Fish | 24% | ± 10% | 50% ± 50% |
| Marine Mammals | 68% | ± 10% | 50% ± 50% |

The assumptions listed in Table 3 were used for the simulations, and are those appropriate to an island which does not have a coral reef or soils primarily derived from marine sediments. Isotope analyses were carried out on nine individuals, yielding mean values of -14.4, +17.4 and +15.7‰ for $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ respectively. Corresponding ranges were -13.3 to -16.2‰, +16.1 to +20.3‰, and +14.1 to +17.5‰. The simulations were therefore designed to find food proportions which could yield isotope results around the mean values, within a certain margin, set to ± 1.5‰ for each isotope, which is a reasonable choice, given the range from one individual to another.

This raises an important point, concerning dietary variability. Seeking average food proportions for a community as a whole, based on average isotope values, is only one way of approaching the problem. Instead food proportions could be estimated for each individual using much closer margins around these filters. After solutions have been found for all the individuals in a study group, one could then, in theory, examine dietary variability in a community.

Moreover, there is a theoretical problem in seeking mean effects (isotope values) from mean causes (food proportions) — if the variability from one individual to another is structured, say along the lines of social status, it may be quite misleading to average out the range of variation, because no individual may have had such a diet.

The same problem is true in reverse: the mean isotope values may not fairly represent anyone in the community either. This problem is analogous to one which arises during the calculation of a multiple correlation matrix with small samples — it is possible to obtain illogical values. For example, variables 1 and 2 might have a positive correlation of say +0.5‰, and variable 1 and 3 also positive at say +0.4‰, while variables 2 and 3 are negative at say -0.3‰. This is an impossible combination, but can easily occur with small samples.

A very similar problem can arise in trying to work out food proportions from isotope values, using results from a small number of individuals, where there is some variability. In the worst case scenario, it might result in an inability to find any combination at all of food proportions which will fit a mean isotope signature for the simple reason that this signature might not have been able to occur in practice.

Unfortunately, the computing required for these simulations is formidable, otherwise it would be advisable to use a strategy based on individuals rather than mean values. However, this problem must be kept in mind, and if there are signs of binodality in the isotope results for a community, the results should be split into groups, and several separate simulations run. In this present test case, the Chatham Islands results are not as tightly clustered as some Pacific groups we have studied, and have an unusual isotope signature for this region. It therefore constitutes a good test for the simulation strategy.

A total of 7,299,277 iterations were tested using the conditions described above, and of these 9,890 satisfied all assumptions and dropped through the Boolean filters, that is one solution was found for every 738 simulations. Considerable experimentation was undertaken, narrowing and widening the filter widths, and also during the ongoing process of collecting background information about the assumptions listed in Table 3. It was found that despite this process of fine-tuning, the resulting overall proportions of the food types did not change markedly, although the rate of finding successful simulations varied considerably. This suggests that the results arrived at are reasonable, given the reliability of the assumptions. The average isotope ratios simulated were:

| | Result Mean | SD | Target Value | Range |
|---|---|---|---|---|
| $\delta^{13}C$ | -13.1 | 0.1‰ | -14.4 | ± 1.5‰ |
| $\delta^{15}N$ | +16.3 | 0.3‰ | +17.4 | ± 1.5‰ |
| $\delta^{34}S$ | +14.4 | 0.2‰ | +15.7 | ± 1.5‰ |

The mean daily energy intake was found to be 2,200 kcal ($\sigma$ = 315), and the daily protein intake was 171 g ($\sigma$ = 20). The mean weight percentages of each food were found to be:

| Food Type | Mean % | σ% | |
|---|---|---|---|
| C3 Plants | 12.2 | 2.7 | |
| C4 Plants | 0.0 | 0.0 | Ignored in present simulation |
| Land Herbivores | 3.6 | 2.9 | |
| Marine Shellfish | 3.5 | 2.4 | |
| Coral Reef Fish | 0.0 | 0.0 | Ignored in present simulation |
| Non-Reef Fish | 33.0 | 10.6 | |
| Marine Mammals | 47.7 | 10.0 | |

The cumulative results for each successful simulation were stored in cells of 1% width and are plotted out in Figure 1.

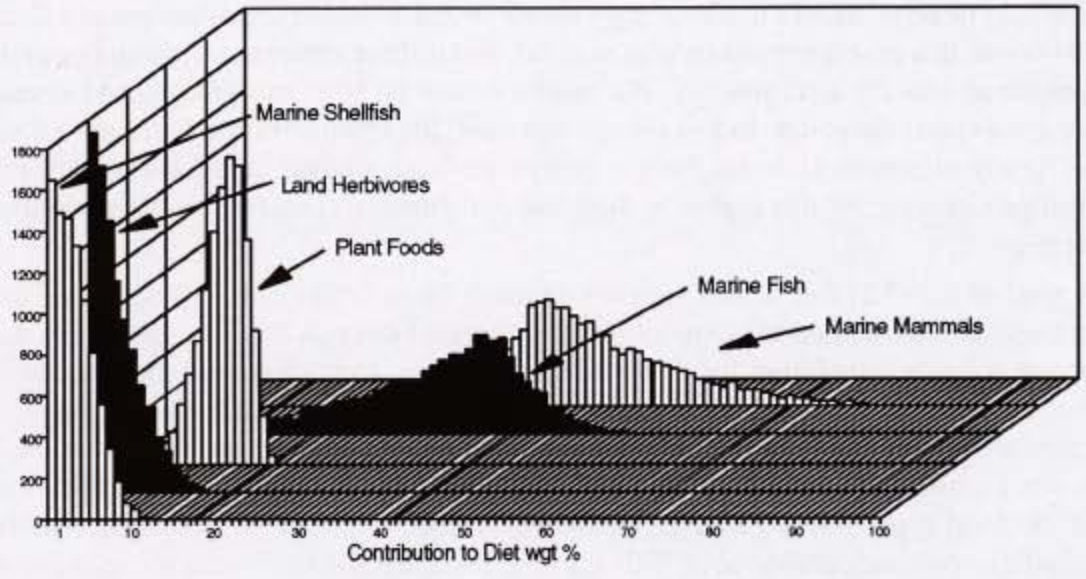


**Figure 1: Proportions of the main items in the diet of prehistoric Chatham Island people based on stochastic simulation algorithm.**

## DISCUSSION AND CONCLUSIONS

The stochastic approach recommended by Minagawa is a significant step forward in the difficult problem of working from effects back to causes in the field of isotope research and dietary reconstruction. In our attempt to implement his suggestion for the types of foods and environmental regimes which are found in the Pacific region we identified a set of 63 assumptions which must be made, and these were further split into those which are appropriate to islands whose soils are substantially derived from marine sediments and those which are not. Although this may seem to be a heavy burden of assumptions, it is a realistic evaluation of the real position, and almost all are inherent in *any* approach taken in this field, not just the stochastic strategy adopted here.

The algorithm was tested using a 'Reverse Experiment' procedure. By taking a diet of known percentage weight composition the isotope composition of human bone was forward calculated from this diet. The algorithm was then employed on this isotope signature to see if the original food composition could be calculated in reverse. The differences between real and calculated food weight percentages for the seven foods were 4.8, 0.1, 4.5, 1.8, 1.5, 1.8 and 1.4% respectively. These were all within acceptable statistical limits, and provide good confidence in the method.

We then applied the algorithm to a prehistoric community from the Chatham Islands. This case study represents an unusual economic adaptation in the Pacific and was deliberately chosen as a suitably extreme test for the simulation strategy. It appeared to work well, in the sense that it produced results which are both plausible and reasonably well constrained.

In the case of $\delta^{13}C$, the food solution arrived at was relevant to a mean value of -13.1‰, which is 1.3‰ lower than the mean value of the group being studied, and is actually slightly lower than the lowest value found in the group of -13.33‰. We believe that the problem here may be caused by carrying out the simulations seeking a pattern of mean isotope values rather than seeking a pattern appropriate for an individual. We tried narrowing down the filter band widths only to find that the rate of finding solutions markedly decreased.

No such problem was encountered with either $\delta^{15}N$ or $\delta^{34}S$. The solution reached for $\delta^{15}N$ was 1.1‰ away from the mean value for the group of people, but there were values lower than the solution for two individuals. Finally, for $\delta^{34}S$, the solution was 1.3‰ lower than the mean value for the group, and once again there was an individual whose value was lower than the solution.

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***Table 1. Assumption Quick-Reference Numbers***

Food Types

1 = C3 Plants
2 = C4 Plants
3 = Land Herbivores
4 = Marine Shellfish
5 = Coral Reef Fish
6 = Non-Reef Fish
7 = Marine Mammals

Isotope values are ‰

| | Isotope Value for Food | | | | | Offset Food to Collagen | | |
|---|---|---|---|---|---|---|---|---|
| Food | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{34}S$ | Protein | kcal | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{34}S$ |
| 1 | 1 | 8 | 15 | 22 | 29 | 36 | 43 | 50 |
| 2 | 2 | 9 | 16 | 23 | 30 | 37 | 44 | 51 |
| 3 | 3 | 10 | 17 | 24 | 31 | 38 | 45 | 52 |
| 4 | 4 | 11 | 18 | 25 | 32 | 39 | 46 | 53 |
| 5 | 5 | 12 | 19 | 26 | 33 | 40 | 47 | 54 |
| 6 | 6 | 13 | 20 | 27 | 34 | 41 | 48 | 55 |
| 7 | 7 | 14 | 21 | 28 | 35 | 42 | 49 | 56 |

Assumptions 57 and 58: Minimax energy intake in kcal/day
Assumptions 59 and 60: Minimax protein intake in g/day
Assumption 61: Fractionation of $\delta^{13}C$ between animal tissue and animal bone collagen
Assumption 62: Fractionation of $\delta^{15}N$ between animal tissue and animal bone collagen
Assumption 63: Fractionation of $\delta^{34}S$ between animal tissue and animal bone collagen

### *Table 2. Marine Dominated Assumptions*

Food Types

1 = C3 Plants
2 = C4 Plants
3 = Land Herbivores
4 = Marine Shellfish
5 = Coral Reef Fish
6 = Non-Reef Fish
7 = Marine Mammals

Note 1: Values marked with an asterisk (*) denote figures which have been converted from published values for bone collagen to values which would be appropriate for flesh.
Note 2: Assumptions 61-63 are used to derive some values in this table, but are not used thereafter in the simulation software.
Note 3: Protein values are g/100g, Energy values are kcal/100g; Isotope values are ‰

| | Isotope Value for Food | | | | | Offset Food to Collagen | | |
|---|---|---|---|---|---|---|---|---|
| Food | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{34}S$ | Protein | Energy | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{34}S$ |
| 1 | -26.0 | +5.8 | +17.0 | 2.2 | 145.0 | +5.0 | +3.0 | -0.5 |
| 2 | -11.5 | +10.0 | +17.0 | 0.4 | 38.0 | +5.0 | +3.0 | -0.5 |
| 3 | -22.6* | +5.4 | +16.5 | 23.1 | 155.0 | +5.0 | +3.0 | -0.5 |
| 4 | -14.0 | +7.2 | +18.6 | 12.9 | 69.0 | +5.0 | +3.0 | -0.9 |
| 5 | -12.6 | +7.9 | +17.7 | 19.7 | 100.0 | +5.0 | +3.0 | -0.9 |
| 6 | -16.5 | +14.0 | +17.7 | 19.7 | 100.0 | +5.0 | +3.0 | -0.9 |
| 7 | -16.8* | +15.7 | +16.8* | 14.0 | 262.0 | +5.0 | +3.0 | -0.9 |

Assumptions 57 and 58: Minimax energy intake = 1800-3700 kcal/day
Assumptions 59 and 60: Minimax protein intake = 25-200 g/day
Assumption 61: $\delta^{13}C$ offset value due to conversion between animal bone collagen and animal tissue = -3.7‰
Assumption 62: $\delta^{15}N$ offset value due to conversion between animal bone collagen and animal tissue = 0.0‰
Assumption 63: $\delta^{34}S$ offset value due to convers‰ion between animal bone collagen and animal tissue = +0.4‰

### *Table 3. Land Dominated Assumptions*

Food Types

1 = C3 Plants
2 = C4 Plants
3 = Land Herbivores
4 = Marine Shellfish
5 = Coral Reef Fish
6 = Non-Reef Fish
7 = Marine Mammals

Note 1: Values marked with an asterisk (*) denote figures which have been converted from published values for bone collagen to values which would be appropriate for flesh.
Note 2: Assumptions 61-63 are used to derive some values in this table, but are not used thereafter in the simulation software.
Note 3: Protein values are g/100g, Energy values are kcal/100g, Isotope values are ‰

| | Isotope Value for Food | | | | | Offset Food to Collagen | | |
|---|---|---|---|---|---|---|---|---|
| Food | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{34}S$ | Protein | Energy | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{34}S$ |
| 1 | -26.0 | +5.8 | +4.9 | 2.2 | 145.0 | +5.0 | +3.0 | -0.5 |
| 2 | -11.5 | +10.0 | +4.9 | 0.4 | 38.0 | +5.0 | +3.0 | -0.5 |
| 3 | -22.6* | +5.4 | +4.4 | 23.1 | 155.0 | +5.0 | +3.0 | -0.5 |
| 4 | -14.0 | +7.2 | +18.6 | 12.9 | 69.0 | +5.0 | +3.0 | -0.9 |
| 5 | -12.6 | +7.9 | +17.7 | 19.7 | 100.0 | +5.0 | +3.0 | -0.9 |
| 6 | -16.5 | +14.0 | +17.7 | 19.7 | 100.0 | +5.0 | +3.0 | -0.9 |
| 7 | -16.8* | +15.7 | +16.8* | 14.0 | 262.0 | +5.0 | +3.0 | -0.9 |

Assumptions 57 and 58: Minimax energy intake = 1800-3700 kcal/day
Assumptions 59 and 60: Minimax protein intake = 25-200 g/day
Assumption 61: $^{13}C$ offset value due to conversion between animal bone collagen and animal tissue = -3.7‰
Assumption 62: $\delta^{15}N$ offset value due to conversion between animal bone collagen and animal tissue = 0.0‰
Assumption 63: $\delta^{34}S$ offset value due to conversion between animal bone collagen and animal tissue = +0.4‰

### *Table 4. Published Isotope Values for Land Herbivores*

Source: Katzenburg 1989: 323, Table 3
Isotope values are ‰

| Location | Sample Number | Common Name | Genus | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{34}S$ |
|---|---|---|---|---|---|---|
| Sth Ontario | 55Ez14 | Deer | *Odocoileus* | -22.8 | +5.4 | - |
| Sth Ontario | 55Ez14 | Deer | *Odocoileus* | -22.3 | - | - |
| Sth Ontario | 55Eg11 | Deer | *Odocoileus* | - 21.7 | +6.4 | - |
| Sth Ontario | 55Ec81 | Deer | *Odocoileus* | -22.2 | +6.2 | - |
| Sth Ontario | 55Ef161 | Deer | *Odocoileus* | -22.2 | +5.4 | - |
| Sth Ontario | 55Ec2 | Deer | *Odocoileus* | -22.3 | +4.5 | - |
| Sth Ontario | Eg16 | Deer | *Odocoileus* | -22.2 | +5.5 | - |
| Sth Ontario | Eg16 | Deer | *Odocoileus* | -22.1 | +5.6 | - |
| Sth Ontario | Eg105 | Deer | *Odocoileus* | -22.3 | +5.2 | - |
| Sth Ontario | Eg105 | Deer | *Odocoileus* | -22.2 | +5.1 | - |
| Means (N=10 and 9) | | | | -22.23 | +5.48 | - |
| Confidence Limits (± SE Mean) | | | | ±0.08 | ±0.19 | - |

[4] Note for Table 5: In the following Tables the term "Unweighted Mean" refers to the mean of all individual figures available, not the average of the reported means. The value given in Table 6 for $\delta^{13}C$, for example, is calculated as the sum with the final three values as (-8.4 x 3) + (-14.1 x 4) + (-13.6 x 6). In cases where a mean is calculated using only one value per species, this is referred to as the "Simple Mean". The reason for having two methods for calculating mean values is that sometimes there is a very large study of one speices, and if an "Unweighted Mean" were calculated in such a case, the overall mean would be dominated by this one species.
In cases where an "Unweighted Mean" has been calculated from all values in the table, including multiple ones designated as N=3, N=4, etc, the corresponding standard error will be a biased estimate of the confidence limits. This is because only the mean value was reported in the case of these multiples samples, the calculated standard deviation is therefore biased, and consequently the Standard Error of the Mean is similarly biased. The general effect of this is that the stated confidence limits will be slightly too small in these cases. The term "Biased SE" is used to denote this case, and "Simple SE" when the "Simple Mean" was calculated.

### *Table 5. Published and Unpublished Isotope Values for Marine Shellfish*

Sources

1. Keegan and DeNiro 1988: 325, Table 2
2. Fry *et al.* 1983: 712, Table 3
3. Sealy *et al.* 1987: 2709, Table 1
4. Lyon, n.d.
5. Peterson *et al.* 1986: 869
6. Kaplan *et al.* 1963: 330

Note: Providenciales is in the Turks and Caicos Islands, isotope values are ‰

| Location | Species | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{34}S$ |
|---|---|---|---|---|
| 1. Providenciales | *Bittium varium* | -10.9 | +3.7 | - |
| 1. Providenciales | *Strombus gigas* | -12.6 | +2.1 | - |
| 2. Torres Strait | *Anadara antiquata* (N=3) | -8.4 | - | - |
| 2. Torres Strait | *Tridacna maxima* | -12.5 | - | - |
| 2. Torres Strait | *Spondylus nicobaricus* (N=6) | -12.4 | - | - |
| 2. Torres Strait | *Pinna* sp. | -13.6 | - | - |
| 2. Torres Strait | *Isognomon isognomon* (N=2) | 15.6 | - | - |
| 3. South-west Cape | *Patella granatina* | - | +8.0 | - |
| 3. South-west Cape | *Patella granularis* | - | +8.4 | - |
| 3. South-west Cape | *Patella argenvillei* | - | +7.2 | - |
| 3. South-west Cape | *Haliotis midae* | - | +7.1 | - |
| 3. South-west Cape | *Choromytilus meridionalis* | - | +8.2 | - |
| 3. South-west Cape | *Choromytilus meridionalis* | - | +8.9 | - |
| 3. South-west Cape | *Choromytilus meridionalis* | - | +8.1 | - |
| 3. South-west Cape | *Choromytilus meridionalis* | - | +8.7 | - |
| 3. South-west Cape | *Choromytilus meridionalis* | - | +8.4 | - |
| 4. Marlborough Sounds | *Perna canaliculus* (N=126) | -18.99 | - | - |
| 4. Marlborough Sounds | *Atrina zelandica* | -19.0 | - | - |
| 4. Marlborough Sounds | *Haliotis iris* | -13.8 | - | - |
| 4. Marlborough Sounds | *Glycymeris laticostata* | -16.0 | - | - |
| 5. Woods Hole | *Mytilus edulis* | - | - | +16.8 |
| 6. Gulf of California | *Haliotis cracherodii* | - | - | +20.9 |
| Simple Means[4] (N=15 and 11) | | -13.98 | +7.16 | +18.56 |
| Simple Confidence Limits (± SE Mean) | | 0.97 | 0.67 | 0.68 |

## *Table 6. Published Isotope Values for Coral Reef Fish*

Sources

1. Reef fish from Grand Bahama Island. Keegan and DeNiro 1988: 326, Table 3
2. Fish from seagrass meadows, Torres Strait. Fry *et al.* 1983: 711, Table 1

Isotope values are ‰

| Species | Common name | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{34}S$ |
|---|---|---|---|---|
| 1. *Haemulon flavolineatum* | Yellow Grunt | -10.5 | +8.1 | - |
| 1. *Haemulon flavolineatum* | Yellow Grunt | -10.5 | +7.7 | - |
| 1. *Haemulon flavolineatum* | Yellow Grunt | -10.9 | +7.2 | - |
| 1. *Haemulon flavolineatum* | Yellow Grunt | -10.3 | +8.2 | - |
| 1. *Haemulon flavolineatum* | Yellow Grunt | -10.5 | +7.9 | - |
| 1. *Haemulon flavolineatum* | Yellow Grunt | -10.9 | +7.2 | - |
| 1. *Haemulon album* | Margate | -11.1 | +6.9 | - |
| 1. *Haemulon parra* | Sailor's Choice | -10.8 | +7.1 | - |
| 1. *Haemulon sciurus* | Blue-stripe Grunt | -11.1 | +7.0 | - |
| 1. *Lutjanus mahogani* | Hog Snapper | -11.2 | +6.2 | - |
| 1. *Lutjanus griseus* | Gray Snapper | -9.9 | +8.2 | - |
| 1. *Lutjanus griseus* | Snapper | -15.7 | +7.8 | - |
| 1. *Lutjanus jocu* | Dog Snapper | -11.9 | +7.9 | - |
| 1. *Lutjanus synagris* | Lane Snapper | -10.1 | +8.6 | - |
| 1. *Epinephelus guttatus* | Nassau grouper | -13.0 | +7.6 | - |
| 1. *Epinephelus striatus* | Red Hind | -12.9 | +7.3 | - |
| 1. *Balistes vetula* | Queen Triggerfish | -11.6 | +7.3 | - |
| 1. *Balistes vetula* | Queen Triggerfish | -11.8 | +8.2 | - |
| 1. *Holocentrus rufus* | Squirrelfish | -11.1 | +7.8 | - |
| 1. *Ocyurus chrysurus* | Yellowtail Snapper | -12.2 | +7.1 | - |
| 1. *Calamus bajonado* | Jolthead Porgy | -10.9 | +6.0 | - |
| 1. *Anisotremus virginicus* | Porkfish | -13.2 | +7.5 | - |
| 1. *Caranx fusus* | Blue Runner Jack | -12.0 | +7.5 | - |
| 1. *Cephalopholis fulva* | Coney | -12.9 | +8.0 | - |
| 1. *Priacanthus cruentatus* | Bigeye | -15.1 | +6.5 | - |
| 1. *Hemiramphus* sp. | Halfbeak | -16.2 | +9.7 | - |
| 1. *Hemiramphus* sp. | Halfbeak | -16.9 | +9.6 | - |
| 1. *Hemiramphus* sp. | Halfbeak | -15.4 | +9.9 | - |
| 1. *Hemiramphus* sp. | Halfbeak | -17.0 | +9.3 | - |
| 1. *Hemiramphus* sp. | Halfbeak | -16.5 | +8.1 | - |
| 1. *Hemiramphus* sp. | Halfbeak | -16.4 | +9.9 | - |

| | | | | |
|---|---|---|---|---|
| 2. ? sp. Bampfield Head (N=3) | ? | -8.4 | - | - |
| 2. ? sp. Friday Passage (N=4) | ? | -14.1 | - | - |
| 2. ? sp. Battery Point (N=6) | ? | -13.6 | - | - |
| Unweighted Means (N=44 and 31) | | -12.58 | +7.85 | +17.7[5] |
| Biased Confidence Limits (± SE Mean) | | 0.35 | 0.18 | - |

[5] See text for a discussion of this value under Assumption 19

## *Table 7. Published Isotopes Values for Non-Reef Marine Fish*

Sources

1.Schoeninger and DeNiro 1984: 632, Tables 1 and 2. Note the original figures reported were from bone collagen, and have been converted in the table below to equivalent flesh values by adding -3.7‰ in the case of $\delta^{13}C$. The adjustment made to $\delta^{15}N$ value is zero (see text).

2.Hobson 1990: 899, Table 1

3. Lyon n.d.

4.Peterson *et al.* 1986: 869

5. Mekhtiyeva *et al.* 1976: 85

Isotope values are ‰

| Species | Common name | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{34}S$ |
|---|---|---|---|---|
| 1. *Scorpaenichthys marmoratus* | Cabezon | -13.7 | +14.9 | - |
| 1. *Katsuwonus pelamis* | Tuna | -17.9 | +11.4 | - |
| 1. *Genyonemus lineatus* | White Croaker | -15.8 | +12.5 | - |
| 1. *Menticirrhus undulaus* | California Corbina | -15.6 | +14.1 | - |
| 1. *Citharichthys xanthostigma* | Longfin Sanddab | -16.4 | +14.8 | - |
| 1. *Holocentrus suborbitalia* | Squirrelfish | -17.3 | +14.4 | - |
| 1. *Strongylura exilis* | Needlefish | -14.8 | +16.0 | - |
| 1. *Porichtys notatus* | Plainfin Midshipman | -18.1 | +13.7 | - |
| 1. *Hyperprosopon argenteum* | Walleye Surfperch | -16.1 | +14.7 | - |
| 1. *Bagre panamensis* | Catfish | -16.7 | +11.1 | - |
| 2. *Cupea pallasii* (N=3) | ? | -17.5 | - | - |
| 2. *Ammodtyes* sp. (N=5) | ? | -17.9 | +14.3 | - |
| 3. *Parika scaber* | Leather-Jacket | -17.4 | - | - |
| 3. *Physiculus bachus* | Red-Cod | -14.9 | - | - |
| 3. *Helicolenus papillosus* | Sea-Perch | -14.4 | - | - |
| 3. *Galeorhinus australis* | School-Shark | -15.2 | - | - |
| 3. *Arripis trutta* | Kahawai | -15.9 | - | - |
| 3. *Pseudolabrus celidotus* | Spotty | -15.4 | - | - |
| 3. Squid | Squid | -17.5 | - | - |
| 3. *Munida gregaria* | Krill | -21.6 | - | - |
| 3. *Thyrsites atun* | Barracouta | -16.0 | - | - |
| 4. *Xiphias gladius* | Swordfish | - | - | +18.2 |
| 5. *Melanogrammus aeglefinus* | Haddock | - | - | +16.9 |
| Simple Means (N=21 and N=15) | | -16.48 | - | +17.73 |
| Simple Confidence Limits (± SE Mean) | | ±0.37 | - | ±0.29 |
| Weighted Mean | | | +13.94 | |
| Biased Confidence Limits (± SE Mean) | | | ±0.34 | |

### *Table 8. Published Isotope Values or C3 Plants and Tubers*

Sources:
1. Keegan and DeNiro 1988: 324, Table 1
2. Kusakabe *et al.* 1976: 436
Isotope values are ‰

| Species | Common name | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{34}S$ |
|---|---|---|---|---|
| 1. *Dioscorea* sp. | Yam | -25.1 | +7.6 | - |
| 1. *Dioscorea* sp. | Red Yam | -26.3 | +3.7 | - |
| 1. *Dioscorea* sp. | White Yam | -27.0 | +5.2 | - |
| 1. *Dioscorea* sp. | Black Yam | -27.3 | +2.8 | - |
| 1. *Xanthosoma* sp. | American Aroid | -26.1 | +4.3 | - |
| 1. *Manihot esculenta* | Manioc | -27.6 | +2.4 | - |
| 1. Unidentified tuber | Eddoe | -24.4 | +3.2 | - |
| 1. *Ipomoea batatas* | Sweet Potato | -25.7 | +3.8 | - |
| 2. *Nothofagus truncata* seedling | Hard Beech | - | - | +13.9 |
| 2. *N. truncata* litter | | - | - | +16.2 |
| 2. *N. truncata* leaves | | - | - | +16.0 |
| 2. *Agathis australis* | Kauri | - | - | +17.7 |
| 2. *Pteridium aquilinum* var. *esculentum* | Fern-root | - | - | +11.9 |
| 2. ? sp. coastal forest roots | | - | - | +16.0 |
| Simple Means (N=8 and 8) | | -26.19 | +4.12 | - |
| Simple Confidence Limits (± SE Mean) | | ±0.39 | ±0.58 | - |
| Marine Dominated Value | | | | +17.0[6] |
| Land Dominated Value | | | | +4.9 |

[6] See text under Assumptions 15a and 15b for an explanation of the values +17.0‰ and +4.9‰

### *Table 9. Published Isotope Values for C4 Plants*

Sources:
1: Keegan and DeNiro 1988: 324, Table 1
2: Present study
3: Quinn 1990: 170, Table 5.1
4: Peterson *et al.* 1985: 1361, Table 1
5: Peterson *et al.* 1986: 868
Isotope values are ‰

| Species | Common name | $\delta^{13}C$ | $\delta^{15}N$ | $\delta^{34}S$ |
|---|---|---|---|---|
| 1. *Zea mays* | Maize | -10.8 | - | - |
| 1. *Zea mays* | Maize | -10.1 | +10.0 | - |
| 2. *Saccharum officinarum* | Sugar Cane | -11.56 | +3.47 | +9.8 |
| 3. *Imperata cylindrica* | Kunai | -10.89 | - | - |
| 4. *Spartina alterniflora* | Marsh grass | -13.10 | +3.8 | - |
| Assumed Means | | -11.5 | +10.0 | |
| Marine Dominated | | | | +17.0[7] |
| Land Dominated | | | | +4.9[7] |

[7]See text under Assumptions 2, 9, 16a, 16b

## *Table 10. Published Nutritional Values for Pacific Foods*

Sources
1. Anon. 1983
2. Milligan *et al.* 1988
3. Smith 1985
4. Waddell 1972: Appendix 5
5. Massal and Barrau 1956: 9, 14, 17, 20, 25, 29, 34
6. Vlieg 1988
7. Hongo and Ohtsuka 1993

Note 1: Protein values are g/100g, and Energy values are kcal/100g
Note 2: Common names are frequently given in sources rather than species names, and the original terminology is followed below
Note 3: The values given for New Zealand shellfish are raw flesh values
Note 4: The values given for Coral Reef Fish are taken from Tables relating to tropical Pacific Island fishes, but which did not specify whether they were reef or non-reef species
Note 5: The values given for Elephant seal, Leopard seal, Fur seal and Sea lion were calculated on the basis of human consumption being 50% meat and 50% blubber
Note 6: Protein values for fish refer to the whole fish
Note 7: Energy values for fish refer to fillet part

| Common Name | Species | Protein | Source | Energy | Source |
|---|---|---|---|---|---|
| **C3 Plants** | | | | | |
| Aibika leaf | *Abelmoschus manihot* | 4.4 | 7 | 46 | 7 |
| Banana | *Musa paradisiaca sapientum* | 1.0 | 5 | 88 | 5 |
| Banana | - | 1.1 | 2 | 79 | 2 |
| Banana | - | 1.1 | 4 | 94 | 4 |
| Banana | *Musa* spp. | 1.2 | 7 | 110 | 7 |
| Breadfruit | - | 1.6 | 5 | 105 | 5 |
| Breadfruit | *Artocarpus communis, altilis, incisus* | 3.1 | 7 | 130 | 7 |
| Canarium almond | *Canarium* spp. | 10.5 | 7 | 527 | 7 |
| Coconut | *Cocos nucifera* | 2.2 | 7 | 189 | 7 |
| Coconut (mature nut) | - | 3.8 | 5 | 350 | 5 |
| Coconut | - | 1.9 | 4 | 230 | 4 |
| Coconut flesh raw | - | 3.2 | 2 | 351 | 2 |
| Coconut milk | - | 0.3 | 2 | 21 | 2 |

| | | | | | |
|---|---|---|---|---|---|
| Cycas | *Cycas circinalis* | 5.9 | 7 | 201 | 7 |
| Famine food | *Amorphophallus campanulatus* | 1.2 | 5 | 79 | 5 |
| Elephant-foot yam | *Amorphophallus campanulatus* | 1.6 | 7 | 89 | 7 |
| Fern leaf | *Dryopteris* spp. *Alsophila* spp. | 4.6 | 7 | 49 | 7 |
| Green Leaves | - | 1.5 | 4 | 23 | 4 |
| Hyacinth Bean | *Lablab purpureus* | 14.8 | 7 | 210 | 7 |
| Kumara, Owairaka red | *Ipomoea batatas* | 2.0 | 2 | 84 | 2 |
| Malay apple | *Eugenia malaccensis* | 0.6 | 7 | 28 | 7 |
| Mangrove fruit | *Bruguiera* spp. | 2.5 | 7 | 75 | 7 |
| Pandanus | *Pandanus julianetti* | 10.7 | 4 | 588 | 4 |
| Coastal pandanus | *Pandanus odoratissima, pulposus* | 1.3 | 7 | 179 | 7 |
| Okari | *Terminalia* spp. | 15.8 | 7 | 461 | 7 |
| Plantain | - | 1.0 | 2 | 122 | 2 |
| Pomelo | *Citrus grandis* | 0.7 | 7 | 39 | 7 |
| Polynesian chestnut | *Inocarpus fagifer, edulis* | 4.8 | 7 | 215 | 7 |
| Puwha | *Sonchus oleraceus* | 2.7 | 2 | 17 | 2 |
| Sago flour | *Metroxylon* spp. | 0.2 | 7 | 287 | 7 |
| Swamp cabbage leaf | *Ipomoea aquatica* | 3.4 | 7 | 30 | 7 |
| Sweet Potato | - | 1.7 | 5 | 100 | 5 |
| Sweet Potato | - | 0.9 | 4 | 150 | 4 |
| Sweet potato | *Ipomoea batatas* | 1.2 | 7 | 122 | 7 |
| Sweet potato leaf | *Ipomoea batatas* | 3.4 | 7 | 41 | 7 |
| Taro | *Colocasia esculenta* | 2.0 | 1 | 113 | 1 |
| Taro | *Colocasia/Xanthosoma* | 1.9 | 5 | 100 | 5 |
| Taro | *Colocasia/Xanthosoma* | 1.4 | 4 | 145 | 4 |
| Taro | *Colocasia esculenta* | 1.5 | 7 | 112 | 7 |
| Taro leaf | *Colocasia esculenta* | 3.4 | 7 | 48 | 7 |
| Taro leaf | - | 3.5 | 5 | - | - |
| Giant taro | *Alocasia macrorrhiza* | 1.5 | 7 | 112 | 7 |
| Winged bean | *Psophocarpus tetragonolobus* | 22.7 | 7 | 287 | 7 |
| Yam | - | 1.9 | 4 | 107 | 4 |
| Yam | - | 2.0 | 5 | 103 | 5 |
| Yam | *Dioscorea* spp. | 2.1 | 7 | 107 | 7 |
| **C4 Plants** | | | | | |
| Pit pit | *Saccharum edule* | 4.1 | 4 | 38 | 4 |
| Coastal pitpit | *Saccharum edule* | 2.9 | 7 | 33 | 7 |
| Highland pitpit | *Setaria palmifolia* | 0.8 | 7 | 25 | 7 |
| Sugar cane | *Saccharum officinarum* | 0.4 | 4 | 38 | 4 |

| | | | | | |
|---|---|---|---|---|---|
| Sugar cane juice | *Saccharum officinarum* | 0.3 | 1 | 73 | 1 |
| Sugar cane | *Saccharum officinarum* | 0.3 | 7 | 65 | 7 |
| **Land Herbivores** | | | | | |
| Bandicoot | *Echymipera* spp. | 21.4 | 7 | 96 | 7 |
| Brush turkey | *Megapodius freycinet* | 20.5 | 7 | 104 | 7 |
| Cassowary | *Casuarius casuarius* | 21.1 | 7 | 109 | 7 |
| Chicken, roasted dark meat | | 23.1 | 2 | 155 | 2 |
| Cuscus | *Phalanger* spp. | 21.7 | 7 | 202 | 7 |
| Dog | - | 21.0 | 3 | 126 | 3 |
| Flying foxes | Various species | 18.6 | 7 | 141 | 7 |
| Pig, leg, roasted | - | 26.9 | 2 | 286 | 2 |
| Pig | *Sus scrofa* | 18.4 | 7 | 230 | 7 |
| Pigeon, roasted flesh | - | 27.8 | 2 | 230 | 2 |
| Pigeons | Various species | 21.7 | 7 | 129 | 7 |
| Pork, fat | - | 10.0 | 4 | 488 | 4 |
| Tortoise | *Chelodina* spp. | 16.3 | 7 | 109 | 7 |
| Wallabies | Various species | 20.8 | 7 | 95 | 7 |
| Wild ducks | Various species | 21.7 | 7 | 117 | 7 |
| **Marine Shellfish** | | | | | |
| Bluff oyster | *Ostrea sinuata* | 12.9 | 6 | 103 | 6 |
| Clam | Family Veneridae | 8.8 | 7 | 59 | 7 |
| Cockle | *Austrovenus stutchburyi* | 8.2 | 2 | 43 | 2 |
| Cockle | *Glycymeris laticostata* | 8.2 | 6 | 43 | 6 |
| Green mussel | *Perna canaliculus* | 11.9 | 6 | 79 | 6 |
| Green mussel | *Perna canaliculus* | 12.9 | 2 | 88 | 2 |
| Horse mussel | *Atrina zelandica* | 14.8 | 6 | 73 | 6 |
| Kina | *Evechinus chloroticus* | 10.8 | 6 | 94 | 6 |
| Mangrove clam | *Gelonia* spp. | 6.9 | 7 | 48 | 7 |
| Oyster | *Tiostrea lutaria* | 10.9 | 2 | 76 | |
| Oyster | *Ostrea* spp. | 10.6 | 7 | 77 | 7 |
| Pacific oyster | *Crassostrea gigas* | 13.1 | 6 | 86 | 6 |
| Pacific shellfish | - | 10.0 | 1 | 70 | 1 |
| Pacific oyster | - | 13.1 | 2 | 86 | 2 |
| Paddle crab | *Ovalipes catharus* | 15.5 | 6 | 74 | 6 |
| Paua | *Haliotis iris* | 20.6 | 2 | 95 | 2 |
| Paua | *Haliotis iris* | 20.8 | 6 | 99 | 6 |
| Pipi | *Paphies australe* | 8.2 | 6 | 41 | 6 |
| Scallop | *Pecten novaezealandiae* | 14.9 | 2 | 80 | 2 |
| Scallop | *Pecten novaezealandiae* | 15.4 | 6 | 83 | 6 |

| | | | | | |
|---|---|---|---|---|---|
| Toheroa | *Paphies ventricosum* | - | - | 14 | 2 |
| Tuatua | *Paphies subtriangulatum* | 16.7 | 6 | 110 | 6 |
| **Squids and Crustaceans** | | | | | |
| Arrow squid | *Notodarus* sp. | 19.2 | 6 | 93 | 6 |
| Broad squid | *Sepiotheutis bilineata* | 19.1 | 6 | 94 | 6 |
| Warty squid | *Morotheusis ingens* | 14.1 | 6 | - | - |
| Blue crab | *Neptunes* spp., *Scylla* spp. | 19.0 | 7 | 113 | 7 |
| Crayfish | *Cherax communis* | 16.4 | 7 | 69 | 7 |
| Prawn | *Macrobrachium* spp. | 13.1 | 7 | 67 | 7 |
| Rock lobster | *Jasus edwardsii* | 21.9 | 6 | 97 | 6 |
| **Coral Reef Fish** | | | | | |
| Fish, marine, lean fillet | | 17.0 | 1 | 73 | 1 |
| Fish, marine, fatty fillet | | 19.0 | 1 | 166 | 1 |
| **Non-Reef Fish** | | | | | |
| Albacore | *Thunnus alalunga* | 26.4 | 2 | 148 | 2 |
| Albacore tuna | *Thunnus alalunga* | 24.0 | 6 | 148 | 6 |
| Alfonsino | *Beryx splendens* | 15.7 | 6 | 194 | 6 |
| Arrow squid | *Nototodarus sloanii* | 19.2 | 2 | 93 | 2 |
| Barracouta | *Thyrsites atun* | 18.4 | 6 | 107 | 6 |
| Barracouta | *Thyrsites atun* | 20.6 | 2 | 112 | 2 |
| Baxters dogfish | *Etmopterus baxteri* | 18.1 | 6 | 79 | 6 |
| Black oreo dory | *Neocyttus* sp. | 16.1 | 6 | 88 | 6 |
| Black slickhead | *Xenodermichthys socialis* | 9.5 | 6 | 45 | 6 |
| Blue moki | *Latridopsis ciliaris* | 19.4 | 6 | 97 | 6 |
| Blue Warehou | *Seriolella brama* | 20.5 | 2 | 116 | 2 |
| Blue cod | *Parapercis colias* | 17.8 | 6 | 80 | 6 |
| Blue-nose warehou | *Hyperoglyphe antarctica* | 18.0 | 6 | 84 | 6 |
| Blue mackerel | *Scomber australasicus* | 19.8 | 6 | 185 | 6 |
| Blue cod | *Parapercis colias* | 18.1 | 2 | 80 | 2 |
| Bluenose | *Hyperoglyphe antarctica* | 19.0 | 2 | 90 | 2 |
| Butterfish | *Odax pullus* | 17.9 | 2 | 80 | 2 |
| Butterfish | *Odax pullus* | 16.7 | 6 | 80 | 6 |
| Cardinal fish | *Epigonus* sp. | 16.9 | 6 | 90 | 6 |
| Common warehou | *Seriolella brama* | 17.5 | 6 | 123 | 6 |
| Eel | *Anguilla australis* | - | - | 92 | 2 |
| Eel | *Anguilla dieffenbachii* | - | - | 43 | 2 |
| Eel | - | 16.6 | 2 | 168 | 2 |
| Elephant fish | *Callorhynchys milii* | 20.3 | 6 | 99 | 6 |
| Frostfish | *Lepidopus caudatus* | 18.6 | 6 | 77 | 6 |
| Garfish | *Hyporhamphus ihi* | 19.8 | 6 | 93 | 6 |

| | | | | | |
|---|---|---|---|---|---|
| Gemfish | *Rexea solandri* | 17.9 | 6 | 104 | 6 |
| Giant stargazer | *Kathetostoma giganteum* | 15.9 | 6 | 90 | 6 |
| Grey mullet | *Mugil cephalus* | 19.5 | 6 | 117 | 6 |
| Groper | *Polyprion oxygeneios* | 19.4 | 2 | 93 | |
| Hake | *Merluccius australis* | 15.3 | 6 | 80 | 6 |
| Hapuku | *Polyprion oxygeneios* | 18.6 | 6 | 95 | 6 |
| Hoki | *Macruronus novaezelandiae* | 17.2 | 2 | 88 | 2 |
| Hoki | *Macruronus novaezelandiae* | 15.4 | 6 | 79 | 6 |
| Jack mackerel | *Trachurus declivis* | 18.6 | 6 | 123 | 6 |
| Javelin fish | *Lepidorhynchus denticulatus* | 13.9 | 6 | 74 | 6 |
| John dory | *Zeus japonicus* | 18.1 | 6 | 89 | 6 |
| John Dory | *Zeus faber* | 20.6 | 2 | 90 | 2 |
| Kahawai | *Arripis trutta* | 19.4 | 6 | 162 | 6 |
| Kahawai | *Arripis trutta* | 21.2 | 2 | 162 | 2 |
| Kingfish | *Seriola grandis* | 20.8 | 6 | 96 | 6 |
| Leatherjacket | *Parika scaber* | 17.2 | 6 | 81 | 6 |
| Lemon sole | *Pelotretis flavilatus* | 18.8 | 6 | 86 | 6 |
| Ling | *Genypterus blacodes* | 19.7 | 2 | 86 | 2 |
| Ling | *Genypterus blacodes* | 18.5 | 6 | 86 | 6 |
| Lookdown dory | *Cyttus traversi* | 17.3 | 6 | 96 | 6 |
| New Zealand sole | *Peltorhamphus novaezeelandiae* | 18.3 | 6 | 88 | 6 |
| Orange roughy | *Hoplostethus atlanticus* | 12.2 | 6 | 59 | 6 |
| Pale ghost shark | *Hydrolagus* sp. | 12.4 | 6 | 80 | 6 |
| Parore | *Girella tricuspidata* | 17.9 | 6 | 88 | 6 |
| Pilchards | *Sardinops neopilchardus* | 19.4 | 6 | 96 | 6 |
| Porae | *Nemodactylus douglasi* | 19.7 | 6 | 115 | 6 |
| Rattail | *Coelorynchus* sp. | 15.3 | 6 | 79 | 6 |
| Rays bream | *Brama brama* | 18.6 | 6 | 97 | 6 |
| Red cod | *Pseudophycis bacchus* | 16.0 | 6 | 70 | 6 |
| Red gurnard | *Chelidonichthys kumu* | 18.6 | 6 | 87 | 6 |
| Red Cod | *Pseudophycis bachus* | 16.9 | 2 | 73 | 2 |
| Ribaldo | *Mora pacifica* | 16.3 | 6 | 78 | 6 |
| Ridge-scaled rattail | *Macrourus carinatus* | 14.3 | 6 | 75 | 6 |
| Rig | *Mustelus lenticulatus* | 20.1 | 6 | 94 | 6 |
| Rock lobster | *Jasus edwardsii* | 23.2 | 2 | 105 | 2 |
| Sand flounder | *Rhombosolea plebeia* | 17.7 | 2 | 80 | 2 |
| Sand flounder | *Rhombosolea plebeia* | 17.6 | 6 | 80 | 6 |
| School shark | *Galeorhinus australis* | 18.5 | 6 | 94 | 6 |
| Sea perch | *Helicolenus papillosus* | 13.8 | 6 | 73 | 6 |
| Silver warehou | *Seriolella punctata* | 15.9 | 6 | 163 | 6 |

| | | | | | |
|---|---|---|---|---|---|
| Silver dory | *Cyttus novaezelandiae* | 17.3 | 6 | 79 | 6 |
| Skipjack tuna | *Katsuwonus pelamis* | 23.4 | 6 | 176 | 6 |
| Slender tuna | *Allothunnus fallai* | 19.5 | 6 | 296 | 6 |
| Smooth oreo dory | *Pseudocyttus maculatus* | 13.7 | 6 | 47 | 6 |
| Snapper | *Pagrus auratus* | 17.9 | 6 | 92 | 6 |
| Snapper | *Pagrus auratus* | 19.2 | 2 | 90 | 2 |
| Sole | *Peltorhamphus novaezeelandiae* | 19.4 | 2 | 88 | 2 |
| Southern blue whiting | *Micromesistius australis* | 18.2 | 6 | 83 | 6 |
| Spiky dogfish | *Squalus acanthias* | 17.2 | 6 | 122 | 6 |
| Swollenhead conger | *Pseudoxenamystax bulbiceps* | 16.6 | 6 | 96 | 6 |
| Tarakihi | *Nemadactylus macropterus* | 18.9 | 6 | 108 | 6 |
| Tarakihi | *Nemadactylus macropterus* | 20.9 | 2 | 107 | 2 |
| Trevally | *Caranx georgianus* | 19.4 | 6 | 106 | 6 |
| Trevally | *Caranx georgianus* | 21.0 | 2 | 109 | 2 |
| White warehou | *Seriollela caerulea* | 13.2 | 6 | 169 | 6 |
| Yellow-eyed mullet | *Aldrichetta forsteri* | 18.2 | 6 | 97 | 6 |
| Yellow-belly flounder | *Rhombosolea leporina* | 18.6 | 6 | 86 | 6 |
| **Marine Mammals, Turtles, Crocodiles, Misc.** | | | | | |
| Crocodile | *Crocodilus porosus* | 15.9 | 7 | 82 | 7 |
| Dolphin | *Delphinus delphis* | 16.0 | 3 | 194 | 3 |
| Elephant seal | *Mirounga leonina* | 13.0 | 3 | 276 | 3 |
| Fur seal | *Arctocephalus forsteri* | 14.0 | 3 | 262 | 3 |
| Leopard seal | *Hydrurga leptonyx* | 13.0 | 3 | 276 | 3 |
| Pilot whale | *Globicephala melaena* | 16.0 | 3 | 194 | 3 |
| Sago grub larva | *Rhynchophorus* spp. | 8.0 | 7 | 182 | 7 |
| Sea lion | *Phocarctus hookeri* | 14.0 | 3 | 262 | 3 |
| Sea turtle | *Chelonia mydas* | 16.2 | 7 | 89 | 7 |
| Turtle | - | 16.0 | 1 | 79 | 1 |

**Keywords:** Pacific, prehistoric diet, stable isotope diet signatures, Carbon-13, Nitrogen-15, Sulphur-34, stochastic simulation

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