Dietary reconstruction of an early to middle Holocene human population from the central California coast: insights from advanced stable isotope mixing models

Seth D. Newsome[a,*], Donald L. Phillips[b], Brendan J. Culleton[c], Tom P. Guilderson[d], Paul L. Koch[a]

[a]*Earth Sciences Department, University of California, 1156 High Street, Santa Cruz, CA 95064, USA*
[b]*U.S. Environmental Protection Agency, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Western Ecology Division, 200 SW 35th Street, Corvallis, OR 97333, USA*
[c]*Pacific Legacy Incorporated, 1525 Seabright Avenue, Santa Cruz, CA 95062, USA*
[d]*Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, Livermore, CA 94551, USA*

Abstract

The inherent sampling and preservational biases of the archaeological record make it difficult to quantify prehistoric human diets, especially in coastal settings, where populations had access to a wide range of marine and terrestrial food sources. In certain cases, geochemical proxies such as stable isotope ratios may be utilized to provide robust estimates on the relative proportions of various food resources consumed by prehistoric populations. The Harkins Slough archaeological site (SCR-60/130) is an early to middle Holocene coastal assemblage located on Monterey Bay in central CA. The carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope composition of human burials and associated archaeofauna excavated from the site were measured for input into a concentration-dependent isotope mixing model that is able to statistically discriminate among multiple (>3) food sources. The human burials segregate into two distinct groups, an early (~ 7000 bp) and middle (~ 4500 bp) Holocene population with significant dietary differences. Stable isotope analyses indicate a 70–84% marine food source contribution for the early Holocene group (EHG), but only a 48–58% marine dietary contribution for the middle Holocene group (MHG). Results also suggest that pinnipeds were an important marine food source for both groups. Modeling results are in agreement with archaeological evidence from southern CA, suggesting that early Holocene coastal populations were highly dependent on marine resources, with the ability to procure both littoral and pelagic species. Further, the use of terrestrial plant sources likely increased over time, with the feasible contribution range doubling from the EHG (4–30%, mean 19%) to MHG (10–52%, mean 38%). This trend is supported by regional archaeological evidence for the advent of technological innovations linked to intensive terrestrial plant processing beginning in the middle Holocene. Methodologically, this work demonstrated the utility of a concentration-dependent stable isotope mixing model in an iterative framework to provide feasible ranges of dietary contribution when the number of food sources is too high to allow a unique solution.
© 2004 Published by Elsevier Ltd.

Keywords: Human paleodiets; Stable isotopes; Isotope mixing models; California coast; Early Holocene

1. Introduction

For decades, researchers have debated when marine resource use intensified along the coast of California.

The traditional paradigm argues for a gradual increase in marine resource use over time, beginning with the exploitation of shellfish in the early Holocene and trending towards the procurement of marine vertebrates such as fish and pinnipeds [39,41,42]. Early groups focused on (or were limited to) intertidal environments and it was only the advent of specialized technologies that allowed populations to exploit coastal pelagic and

---

offshore ecosystems. This view has recently been challenged by archaeological evidence from the Channel Islands off southern California, where early Holocene (10,000–8000 bp) coastal groups procured a variety of marine vertebrates using a range of sophisticated technologies [20,23,53,54,69]. Still, a more diverse marine resource base in people inhabiting offshore islands is perhaps unsurprising, given that these islands can only be reached by boating across sometimes rough water with strong currents. The lack of resources from terrestrial sources on these island sites is, likewise, unremarkable. Assessing the intensification of marine resource use more generally will require study of mainland coastal sites, where people had access to a greater diversity of potential food resources.

Recent research along the Santa Barbara mainland coast shows that early to middle Holocene coastal groups (8000–6000 bp) consumed a variety of marine and terrestrial resources, with emphasis on the procurement of terrestrial plants and shellfish [16,22]. By 6000 bp, shifting environmental conditions and population growth appear to have led to an increase in hunting and fishing, which persisted into the late Holocene in coastal southern California [22]. Unfortunately, the early to middle Holocene archaeological record from central and northern California is relatively poor in comparison to the Santa Barbara Channel. With the exception of Duncan's Point Cave in Sonoma County [60,71] and a few sites around Monterey Bay [8,30], quantifiable early to middle Holocene dietary data from the region are lacking.

The Harkins Slough archaeological site (CA-SCR-60/130) is a coastal site near Watsonville, Santa Cruz County, California. The site sits on terraced Holocene sand dunes at the northern margin of the Pajaro River floodplain, near the confluence of Watsonville and Harkins sloughs, approximately 1.6 km east of the Pacific coast (Fig. 1). Prior to agricultural alteration, the area was dominated by sloughs and wetlands influenced by tides from adjacent Monterey Bay. Archaeological testing and data recovery excavations were conducted by Pacific Legacy Inc. in 1999 and 2000 to mitigate impacts of a pipeline installation for the Harkins Slough local water supply project. Excavations recovered several articulated human burials, a diverse assemblage of ground and flaked stone tools, and vertebrate and shellfish dietary remains [18].

The historically known aboriginal inhabitants of the Monterey Bay region were part of the Ohlone, or Costanoan language family. At European contact, the Ohlone were hunter–gatherers, moving from semi-permanent villages into surrounding areas on a seasonal basis to collect food resources. Based on archaeofauna recovered from mid- to late Holocene sites in the region [7,12,28,29,56,71], food items included terrestrial mammals (e.g., deer, elk, antelope, rabbit) and a wide array
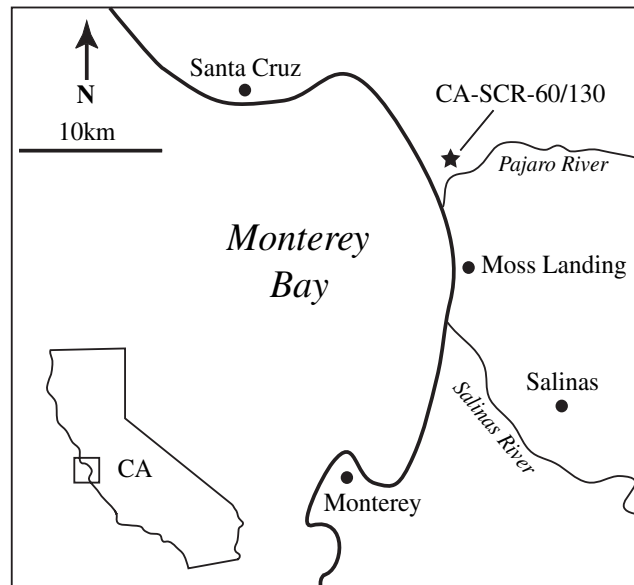

Fig. 1. Location of the Harkins Slough archaeological site (CA-SCR-60/130).

of terrestrial plants, including seeds (e.g., dock, chia), nuts (e.g., acorn, pine, hazelnut), and leafy plants (e.g., purslane, amaranth). Marine resources were also an important subsistence base, including marine fish (e.g., elasmobranchs, surfperch, rockfish, clupeids), shellfish (e.g., abalone, mussel, clam), and marine mammals (e.g., seal, sea lion, sea otters).

While the characterization of ancient diets is important, the quantification of various dietary sources is difficult using traditional archaeological techniques due to an assortment of sampling and preservational biases. In many cases, only a small portion of an archaeological site is excavated, providing a relatively limited representation of the range and/or quantity of archaeofauna in a given assemblage. Furthermore, if individual sites are occupied on a seasonal basis and used to procure/process a particular resource, it is difficult to assess overall resource use when examining material from only one site. In addition, the remains of small vertebrates (e.g., fish) may elude collection depending on the method of recovery.

Stable isotope analysis of human remains and associated archaeofauna provides a direct measurement of diet and is an established method for evaluating the relative proportions of food resources consumed by human populations [33,38,43,50,58,59,70]. Likewise, isotopic analysis of human bone collagen has been used to assess the relative percentage of marine and terrestrial resources in the diets of prehistoric, historic, and modern populations [13,14,43,59,73]. Each of these examples utilized standard linear mixing models, in which distinct isotopic signatures were available for one or two-isotope systems, limiting the number of food sources one can discriminate among in characterizing dietary sources

[46,61]. None of these studies attempted to further constrain the relative inputs of various marine or terrestrial dietary components, such as the relative contribution of shellfish versus pinnipeds in prehistoric diets.

In this study, we determine the stable carbon and nitrogen isotope compositions of prehistoric human bone collagen and use a mixing model to quantify the relative proportions of various food resources in prehistoric human diets. The mixing model is a combination of the IsoConc concentration-dependent isotope model developed by Phillips and Koch [47] with the IsoSource model developed by Phillips and Gregg [48], which assesses the distribution of possible food source contributions to complex human diets where, in this case, a unique solution is mathematically impossible. Our objectives in this paper are threefold. First, we introduce this new combined approach to modeling diets using stable isotope data. We then use the model to better constrain the relative contributions of various food sources to the diets of the two human groups from SCR-60/130. Finally, we consider the implications of our result for ideas about the timing of marine resource intensification.

2. Human burials

Samples of bone collagen for stable isotope and radiocarbon analysis were obtained from nine individuals with the permission of the Most Likely Descendent designated by the California Native American Heritage Commission. We have directly dated, via AMS ^{14}C analysis, all nine individuals and five archaeofaunal elements from the site (Table 1). Where appropriate, we have applied a regional reservoir age (ΔR) of 250 ± 35 years to conventional $\delta^{13}C$-corrected ^{14}C ages while varying the percentage of marine carbon in our correction to report the calibrated 2σ age range for each sample [64,65]. The percentage of marine carbon for each human group is estimated using results of the IsoSource model described below. The inhabitants and fauna from SCR-60/130 date to ∼4500−7700 bp, making the human remains from Harkins Slough among the oldest known burials from the central or northern California coast. The human burials segregate into two groups, with two individuals that date to ∼4500 bp and another group of seven individuals that date to ∼7000 bp. For convenience, we will refer to these two groups as the middle Holocene group (MHG) and early Holocene group (EHG), respectively.

3. Methods and materials

For stable isotope analysis, long bone and cranial fragments (∼50−100 mg) were cleaned of sediment and demineralized in 0.5 N hydrochloric acid (HCl) for

∼12−15 h at 5 °C. The resulting material was treated repeatedly with a methanol/chloroform/water (2:1:0.8) mixture to remove lipids and then freeze-dried. Dried samples (∼1.5 mg) were sealed in Sn boats and then analyzed using a Carlo-Erba elemental analyzer interfaced with an Optima gas source mass spectrometer (Departments of Earth and Ocean Sciences, University of California, Santa Cruz). Results are expressed as δ values, such that $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) − 1] \times 1000$, where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratios of the sample and standard, respectively. The standards are Pee Dee Belemnite limestone for carbon and atmospheric N_2 for nitrogen. The units are expressed as parts per thousand or per mil (‰). Repeated measurements of a gelatin standard ($n = 25$) yielded a $1\sigma < 0.2$‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

For AMS ^{14}C analysis, raw bone samples were crushed and demineralized in 0.5 N HCl at 5 °C for ∼12−15 h. The resulting organic matter was gelatinized in 0.1 N HCl at ∼60 °C for 12−15 h. Gelatinized samples were filtered using glass microfibre filters to remove large particulate matter. The resulting mixture was then ultra-filtered using centrifugal filters to remove low molecular weight (<30 kDa) collagen strands, and vacuum-concentrated [10]. Collagen was converted to CO_2 via combustion and graphitized for AMS analysis.

Depending on the age and health of the individual, bone collagen is completely replaced on the order of several years to over a decade; thus we are evaluating an average of diet over the last several years before death [63,66]. As a control for diagenetic modification of bone collagen isotope values, we measured the carbon-to-nitrogen (C/N) ratios of each sample to test the possibility that isotopic values were altered postmortem. The C/N ratios of these samples are 2.8−3.0, well within the range that characterizes unaltered protein [3].

4. Dietary reconstruction via IsoSource

In a standard linear isotope mixing model, the number of isotope systems (e.g., $\delta^{13}C$, $\delta^{15}N$) utilized (*n*) will allow one to uniquely determine the relative contributions of at most $n+1$ sources to the mixture [46,61]. For example, a two-isotope system can be used to uniquely determine the relative contributions of three dietary sources. Often, problems arise when evaluating omnivorous human diets, which generally include a wide variety of food sources, because the number of sources often exceeds the number of isotope systems needed to differentiate among sources uniquely. To cope with this problem, we use the source-partitioning model (IsoSource) outlined in Phillips and Gregg [48] to statistically constrain the relative proportions of various sources to human diets. IsoSource evaluates all biomass combinations of each source (from 0−100%) in

Table 1
AMS ^{14}C results on human burials and associated fauna from CA-SCR-60/130

Sample name	Lab #	Species	^{14}C age bp ($\pm 1\sigma$)	ΔR ($\pm 1\sigma$)	%Marine C	2σ calibrated age range (bp)
60-HS-002	LLNL-75995	*Homo sapiens*	4370 (50)	250 (35)	(50−**56**−61)	4390−4780
60-HS-003	LLNL-75996	*Homo sapiens*	4210 (60)	250 (35)	(50−**56**−61)	4100−4500
60-HS-001	LLNL-75994	*Homo sapiens*	6570 (50)	250 (35)	(73−**78**−84)	6790−7140
60-HS-004	LLNL-75997	*Homo sapiens*	7060 (100)	250 (35)	(73−**78**−84)	7270−7610
60-HS-005	LLNL-75998	*Homo sapiens*	6740 (60)	250 (35)	(73−**78**−84)	6980−7280
60-HS-006	LLNL-75999	*Homo sapiens*	6470 (50)	250 (35)	(73−**78**−84)	6680−6950
60-HS-007	LLNL-76000	*Homo sapiens*	6490 (50)	250 (35)	(73−**78**−84)	6720−6990
60-HS-008	LLNL-98351	*Homo sapiens*	6535 (45)	250 (35)	(73−**78**−84)	6750−7010
60-HS-009	LLNL-98352	*Homo sapiens*	6540 (70)	250 (35)	(73−**78**−84)	6720−7140
60-CE-001	LLNL-85666	*Cervus elaphus*	5920 (40)	−	−	6640−6850
60-ZC-003	LLNL-85654	*Zalophus californianus*	5475 (50)	250 (35)	100	5460−5700
60-TU1-L7	BETA-172030	*Protothaca staminea*	6600 (60)	250 (35)	100	7400−7170
60-TU5-L2	BETA-172031	*Protothaca staminea*	6460 (50)	250 (35)	100	7000−7280
60-TU5-L6	BETA-172032	*Protothaca staminea*	6630 (50)	250 (35)	100	7220−7420

^{14}C ages have been δ^{13}C-corrected. A regional reservoir age (ΔR) of 250 (± 35) years has been applied when necessary. The range and mean percent marine carbon for the human burials is estimated using results from the IsoSource concentration-dependent mixing model. Only the mean percent marine carbon value (bold) for each group was used to calibrate ^{14}C ages. Radiocarbon analyses were performed under the auspices of the U.S. Department of Energy by the University of California Lawrence Livermore National Laboratory (contract W-7405-Eng-48).

user-defined increments (in this case, 2%) to identify source combinations that sum to the known isotopic signature of the mixture (in this case, human bone collagen) to within a prescribed small tolerance (in this case, ± 0.1‰). We then create a distribution of the frequency and range of potential source contributions. IsoSource does not offer a unique solution, but it does allow evaluation of the statistical constraints on the relative contributions of dietary sources.

Another complication in the application of isotope mixing models is the assumption (often unstated) that the proportional contribution of a source to the mixture is similar for each element [47]. This assumption is reasonable if the elemental concentrations of each source are similar and if they are of equal digestibility (e.g., for animals on all meat or all plant diets). In human diets, however, sources can have dramatically different elemental concentrations. For example, terrestrial plants generally have low [N] relative to [C], so they may provide much lower proportions of N than C to diet. The IsoConc concentration-dependent mixing model developed by Phillips and Koch [47] incorporates both isotopic composition and elemental concentrations to determine the proportional dietary contributions of C, N, and biomass for each food source. We have modified the linear mixing IsoSource program presented in Phillips and Gregg [48] to incorporate concentration-dependence [47] into our solutions. This concentration-dependent IsoSource model assumes that the contribution of each source is proportional to the isotope value times the elemental concentration assimilated from the source. Thus, for each combination of food source biomass contributions tested (which each sum to 100%), the C and N contributions for each food source i ($f_{C,i}$ and $f_{N,i}$) were computed as

$$f_{C,i} = \frac{f_{B,i} \times [C]_i}{\sum_i (f_{B,i} \times [C]_i)} \quad \left. \begin{array}{l} \\ \\ \end{array} \right| \text{ for all food sources } i$$

$$f_{N,i} = \frac{f_{B,i} \times [N]_i}{\sum_i (f_{B,i} \times [N]_i)}$$

where $f_{B,i}$ represents the fraction of biomass contributed to the diet by food source i, and $[C]_i$ and $[N]_i$ represent the assimilated C and N concentrations in the food source i. Food source combinations were considered feasible solutions if the predicted human isotopic signatures $\delta^{13}C_M$ and $\delta^{15}N_M$:

$$\delta^{13}C_M = \sum_i (f_{C,i} \times \delta^{13}C_i)$$

$$\delta^{15}N_M = \sum_i (f_{N,i} \times \delta^{15}N_i)$$

matched the observed signatures within a tolerance of ± 0.1‰. To estimate the assimilated elemental concentration, we must measure (or estimate) the elemental concentrations in different foods, and then use the abundant literature on the digestibility of foods to account for differential assimilation [36].

It should be noted that this mixing model, like others routinely used in stable isotope analysis, assumes homogenization of dietary sources in the consumer's body prior to tissue synthesis [47]. Thus, for example, it does not account for preferential routing of dietary proteins and lipids to synthesis of body proteins and lipids, respectively, if it was present [2,24,37]. However, standard linear mixing models also confound this possible effect with artifacts due to differential elemental concentrations among food sources [47]. For

a controlled feeding study on mink, standard linear mixing models failed to reproduce the known dietary proportions [6]. However, a concentration-dependent model (as we use here) was found to accurately reproduce the diet, arguing that this effect was much larger than effects due to preferential substrate routing [36,47].

5. Isotope values and C/N ratios of dietary sources

We chose seven end-member food sources for input into the IsoSource program to represent the range of foods available to coastal Californians. Estimated isotope values for each source are presented in Fig. 2 and Table 2. The isotope values of the food sources were estimated in a variety of ways. Isotope values of modern marine fish and shellfish were measured to establish end-member values for these food sources [67]. To estimate Holocene $\delta^{13}C$ values from these modern samples, we corrected for the Suess effect (the isotopic depletion of surface carbon reservoirs due to the burning of fossil fuels) by adding 1‰ to measured values [11,51,62]. We assumed modern $\delta^{15}N$ values for marine fish and shellfish tissue were applicable to the Holocene. The Toperoff [67] data for modern marine fish do not include data for salmon, expected to have higher $\delta^{13}C$ and $\delta^{15}N$ values than the relatively small schooling fish species included in her study. However, archaeofaunal analysis reveals that salmon were a relatively minor component of fish remains excavated from regional sites [28]. Isotope values for terrestrial mammal tissue were estimated using measured values of archaeofaunal bone

collagen from the site. Bone collagen $\delta^{13}C$ values were assumed to be 4‰ higher than associated muscle tissue carbon values, whereas muscle $\delta^{15}N$ values were assumed to be the same as those of collagen [2]. Isotope values for terrestrial plants were estimated using the measured isotopic values of deer and elk bone collagen from the site. For carbon, the $\delta^{13}C$ value of the plants consumed by terrestrial herbivores was assumed to be 5‰ lower than measured bone collagen $\delta^{13}C$ values, whereas the $\delta^{15}N$ value of herbivore diets was assumed to be 3‰ lower than bone collagen $\delta^{15}N$ values [35,37]. Likewise, the $\delta^{13}C$ and $\delta^{15}N$ values of human diets were assumed to be 5‰ and 3‰ lower, respectively, than measured bone collagen values. These corrections ensure all isotope data are reported in Holocene 'diet' space for input into the IsoSource model.

Estimating the isotopic and elemental composition of pinniped tissue was more complex, as we attempted to account for the consumption of both muscle and blubber. As for terrestrial meat, we used archaeofaunal bone collagen to establish this dietary component. We measured the $\delta^{13}C$ value of modern pinniped tissues from Monterey Bay ($n = 5$), and determined that, on average, blubber was ~4‰ lower than muscle, or ~8‰ lower than bone collagen (Appendix A). We assumed that local prehistoric human populations consumed both tissues at a mixture of 60:40, which is approximately the ratio (by weight) of protein-to-fat in pinniped soft tissues [17]. The fractionation between bone collagen and bulk pinniped soft tissues would then be $-5.6‰$ ($= -4 \times 0.6 + -8 \times 0.4$), so we subtracted this amount from archaeofaunal bone collagen $\delta^{13}C$ values
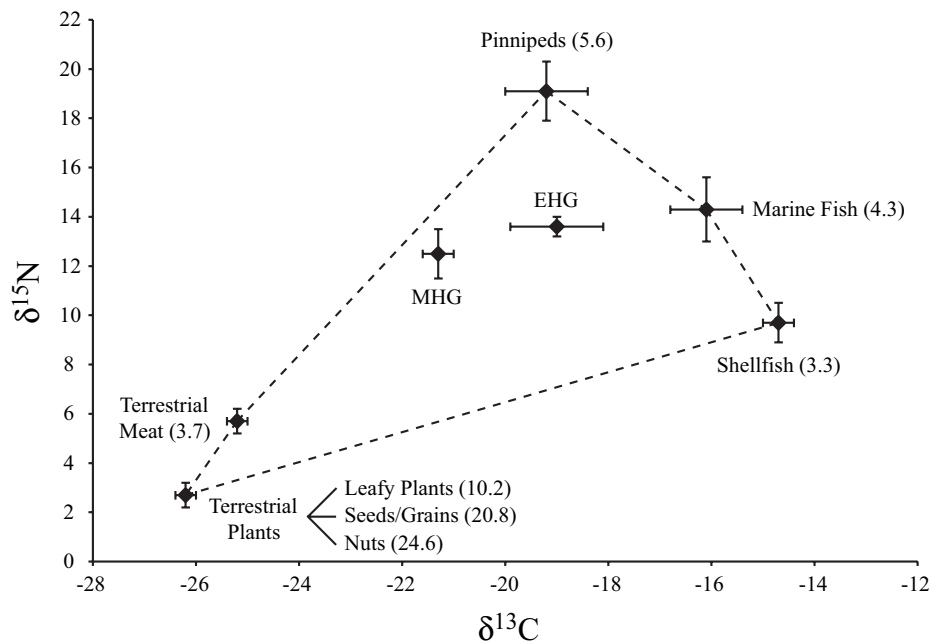

Fig. 2. Mean isotopic composition ($\pm 1\sigma$) of food sources and human groups used in modeling. Numbers in parentheses are the associated C/N ratios of each food source.

Table 2
Isotope data used in modeling

Diet	$\delta^{13}C$	$\delta^{15}N$	Data for estimates	Assumptions
Marine fish$^\phi$ (24)	−16.1 (0.7)	14.3 (1.3)	Modern nearshore marine fish muscle	1,3
Shellfish (8)	−14.7 (0.3)	9.7 (0.8)	Modern CA mussel tissue	1,3
Pinnipeds* (14)	−19.2 (0.8)	19.1 (1.2)	Holocene pinniped bone collagen	2,3
Terrestrial meat (8)	−25.2 (0.2)	5.7 (0.5)	Holocene deer/elk bone collagen	2,3
Terrestrial plants	−26.2	2.7	Holocene deer/elk bone collagen	4,5
Early Holocene humans (7)	**−19.0 (0.9)**	**13.6 (0.4)**	Holocene human bone collagen	4,5
Middle Holocene humans (2)	**−21.3 (0.3)**	**12.5 (1.0)**	Holocene human bone collagen	4,5
Assumptions:	(1) $\delta^{13}C_{\text{Holocene muscle}} = \delta^{13}C_{\text{modern muscle}} + 1$			
	(2) $\delta^{13}C_{\text{muscle}} = \delta^{13}C_{\text{collagen}} - 4$			
	(3) $\delta^{15}N_{\text{soft tissue}} = \delta^{15}N_{\text{collagen}}$			
	(4) $\delta^{13}C_{\text{diet}} = \delta^{13}C_{\text{collagen}} - 5$			
	(5) $\delta^{15}N_{\text{diet}} = \delta^{15}N_{\text{collagen}} - 3$			

Mean isotope composition ($\pm 1\sigma$) of food sources and human groups used in modeling. Assumptions used regarding metabolic fractionations and the 'Suess' effect are listed. The pinnipeds (*) $\delta^{13}C$ value has been corrected assuming a 60:40 (muscle-to-blubber) food source contribution [ϕ−45].

to estimate the $\delta^{13}C$ value of consumed pinniped tissue. We found negligible differences between modern muscle and blubber $\delta^{15}N$ values, as is the case for muscle versus bone collagen [35], so we used the measured collagen $\delta^{15}N$ values from archaeofaunal bone as a proxy for the $\delta^{15}N$ value of pinniped tissues. Likewise, we also analyzed the [C] and [N] of pinniped blubber and muscle tissues from modern pinnipeds to estimate suitable mean elemental concentrations. As expected, blubber had higher [C] and lower [N] than associated muscle (Appendix A). The ingested pinniped [C] and [N] have been corrected assuming a 60:40 muscle-to-blubber contribution.

Elemental concentrations for food sources other than pinnipeds were determined as follows. For shellfish, we measured %C and %N for California mussels (*Mytilus californianus*) collected near Santa Cruz, CA. Elemental concentrations of all other sources were estimated using food composition data from the USDA Nutrient Database (Table 3; 68). The calculations made the following assumptions about food stoichiometry (wt %): protein,

52% carbon, 16% nitrogen; lipid, 75% carbon; carbohydrate (including fiber), 45% carbon [55].

Finally, in order to estimate the [C] and [N] of assimilated biomass, we corrected for differences in the digestibility of different diet macromolecular constituents [36]. We assumed that animal tissue (both fat and protein) was 100% digestible. For terrestrial plants, we make the following assumptions regarding digestibility: protein [C] and [N], 90%; lipid and carbohydrate [C], 100%; fiber, 0% [15,52].

Overall, meat source C/N ratios are less variable than those for plant foods (Table 3). This is in response to the lower variability in [C] in meat relative to plant food sources. Among animal food sources, the outlier C/N values (5.6) and concentration data for pinnipeds can be attributed to the assumption of a 60:40 mixture of muscle and blubber tissue (Appendix A). On the other hand, despite low variability in digestible [N] among plant food sources, the high variability in digestible [C] leads to a wide range of C/N ratios (Table 3). The sources of high variability in [C] among plant foods are

Table 3
Diet composition and digestibility data used in modeling

Diet	Source	Protein N	Protein C	Lipid C	Carb C	Digestible [C]	Digestible [N]	Digestible C/N
Marine fish	Rockfish, surfperch anchovy, shark, etc.	12.4	40.3	12.9	0	53.2	12.4	4.3
Shellfish	CA mussel*	N/A	N/A	N/A	N/A	42.6	12.8	3.3
Pinnipeds	CA sea lion*, northern elephant seal*	N/A	N/A	N/A	N/A	58.1	10.3	5.6
Terrestrial meat	Deer, elk, antelope	14.1	45.9	5.7	0	51.6	14.1	3.7
Leafy plants	Dock, purslane, amaranth	4.2	13.8	3.9	22.6	38.9	3.8	10.2
Nuts	Acorn, pinenut, hazelnut	2.7	8.7	37.9	13.4	59.1	2.4	24.6
Seeds and grains	Chia, amaranth, quinoa	2.6	8.3	10.3	30.0	47.8	2.3	20.8

Food composition from USDA Nutrient Database and modern samples (*) when locally available. Units: g X/100 g dry matter for first four variables; g X/100 g digested dry matter for last three. USDA NDB#: rockfish 15070; surfperch 15060; anchovy 15001; shark 15095; mackerel 15050; croaker 15020; chinook salmon 15078; deer 17164; elk 17166; antelope 17144; dock 11616; purslane 11427; amaranth leaves 11003; acorn 12058; pinenut 12147; hazelnut 12120; chia seed 12006; amaranth seed 20001; quinoa 20035.

differences in the concentration of digestible macromolecules as well as differences in [C] among these macromolecules. Nuts (e.g., acorns and pinenuts) contain a considerable amount of carbon-rich lipids, whereas seeds and grains (e.g., chia and amaranth) contain relatively high concentrations of carbohydrates, which have lower carbon concentrations. Leafy plants contain substantial amounts of non-digestible fiber, so that the digestible carbon concentration is more strongly influenced by leaf proteins, again with a relatively low [C].

6. IsoSource results

Table 4 presents the IsoSource results for the biomass, carbon, and nitrogen proportions for each of the seven food sources and three aggregate categories. There were 11,345 feasible combinations of the seven food sources that reproduced the observed $\delta^{13}C$ and $\delta^{15}N$ signatures in the EHG population within a 0.1‰ tolerance, and 35,021 such combinations for the MHG population. The range of possible values for each source is statistically described as that which falls within the 1st (minimum) and 99th (maximum) percentile. This approach covers 98% of the possible values and does not extend the feasible range to include the small amount of data on the tails of each distribution [48]. While there is a wide range of feasible solutions for individual food sources, comparisons between the two human groups can be made based on the end-member values that define the 1st and 99th percentile. For

instance, the range (and mean) of possible solutions for the pinniped biomass percentage represents a considerable proportion of the total biomass percentage and does not change between the EHG and MHG. Interestingly, the pinniped food source is the only source whose minimum values (1st percentile) do not equal zero. Furthermore, the ranges (and means) of feasible solutions for marine fish and shellfish decrease over time. The maximum value (99th percentile) for marine fish shifts from 68% (EHG) to 44% (MHG) while the maximum value for shellfish shifts from 36% (EHG) to 24% (MHG). In contrast, the maximum biomass percentage values (and means) for terrestrial meat, leafy plants, seeds/grains, and nuts all increase from the EHG to the MHG.

Since the feasible ranges of dietary proportions are relatively large for each of the individual sources, we aggregated the sources into three distinct categories (Table 5). For each feasible combination of food sources, the marine aggregate is the sum of the shellfish, marine fish, and pinniped contributions. Likewise, for each feasible source combination the terrestrial plant aggregate is the sum of the contribution for the three plant types while the terrestrial meat aggregate only includes the terrestrial meat contribution from the IsoSource results. In this way we generated distributions of the feasible combinations of aggregated marine, terrestrial plant, and terrestrial meat food sources ($n = 11,345$ for EHG and $n = 35,021$ for MHG). This process was performed three times, using the biomass, C, and N source distributions from the mixing model.

Table 4
IsoSource result: ranges and means of source distributions

Source	Group	Biomass %			Carbon %			Nitrogen %		
		1%	Mean	99%	1%	Mean	99%	1%	Mean	99%
Marine fish	EHG	0	**36**	68	0	**37**	68	0	**44**	87
	MHG	0	**18**	44	0	**18**	44	0	**27**	72
Shellfish	EHG	0	**14**	36	0	**12**	31	0	**18**	47
	MHG	0	**9**	24	0	**8**	20	0	**14**	41
Pinnipeds	EHG	4	**26**	48	4	**29**	55	4	**26**	47
	MHG	6	**27**	48	6	**30**	53	8	**32**	46
Terrestrial meat	EHG	0	**4**	16	0	**4**	16	0	**6**	20
	MHG	0	**9**	30	0	**9**	29	0	**14**	40
Leafy plants	EHG	0	**7**	24	0	**5**	19	0	**3**	9
	MHG	0	**12**	40	0	**9**	33	0	**6**	20
Nuts	EHG	0	**6**	20	0	**7**	22	0	**1**	5
	MHG	0	**13**	38	0	**14**	42	0	**4**	12
Seeds and grains	EHG	0	**7**	24	0	**6**	22	0	**2**	6
	MHG	0	**13**	42	0	**12**	40	0	**4**	13
Marine	EHG	70	**77**	84	73	**78**	84	79	**90**	95
	MHG	48	**54**	58	50	**56**	61	57	**73**	85
Terrestrial plants	EHG	4	**19**	30	3	**18**	28	1	**5**	10
	MHG	10	**38**	52	10	**36**	50	3	**13**	23
Terrestrial meat	EHG	0	**4**	16	0	**4**	16	0	**6**	20
	MHG	0	**9**	30	0	**9**	29	0	**14**	40

Range of biomass, carbon, and nitrogen proportions for each of the seven individual food sources and three aggregate sources for both the early and middle Holocene groups. Each distribution is defined by the means, 1st and 99th percentile values which cover 98% of all possible solutions.

Table 5
Biomass percentage of diet

(A) Leafy plants	(B) Nuts	(C) Seeds and grains	(D) Pinnipeds	(E) Shellfish	(F) Marine fish	(G) Terrestrial meat
6	18	2	6	2	66	0
	(A + B + C) Terrestrial plants 26			(D + E + F) Marine 74		(G) Terrestrial meat 0

Calculation of dietary contributions of three aggregate food groups (terrestrial plants, marine, terrestrial meat) from the seven individual food sources. This example is for one of the 11,345 feasible dietary biomass solutions for the Early Holocene Group. The procedure is repeated for each solution ($n = 11,345$ for Early Holocene Group) to generate the distribution of feasible terrestrial plant, marine and terrestrial meat biomass contributions to the diet. Similar calculations can be made for C and N contributions.

The range and mean values of the biomass distributions allow us to evaluate the relative proportions of the three dietary aggregates between the early and late Holocene group (Fig. 3). The MHG consumed a lower proportion of marine foods, with concomitant increases in terrestrial plants and/or meat sources, in comparison to the EHG. There is no overlap in the range of values for the marine source distributions between the MHG (48−58%) and EHG (70−84%) and the mean biomass proportions are considerably different, 54% versus 77%, respectively. On the other hand, there is some overlap in the distributions of terrestrial plant values between the two groups, but the mean value of the MHG (38%) is twice that of the EHG (19%). Likewise, the possible range in terrestrial meat values nearly doubles between the EHG (0−16%) and the MHG (0−30%). These results suggest the likelihood of increases in consumption of both terrestrial plant and meat sources through time. Although each of these two increases cannot definitively be concluded due to the overlap in EHG and MHG ranges, terrestrial food sources (plants and meat together) did increase markedly from a range of 16−30% for EHG to 42−52% for MHG.

The range of carbon and nitrogen distributions for each aggregate food source reveals the utility of a concentration-dependent mixing model (Table 4). For example, the nitrogen contribution of marine sources is greater than their total biomass contribution, showing that the proportion of nitrogen derived from marine sources (nitrogen-rich foods) is greater than the proportion of carbon derived from that food source. Likewise, the nitrogen contribution of terrestrial plants is less than their total biomass contribution, because plants (carbon-rich foods) have lower nitrogen concentrations relative to carbon, and contribute less nitrogen to total biomass. A standard linear mixing model would not account for the relative amount of C and N derived from each source. Rather, it would assume that the concentrations are equal among sources for the two elements, which would ultimately bias the relative contribution of each source.

The aggregation of individual food sources, after the mixing analysis, into logical food groups (marine, terrestrial plants, terrestrial meat) had two advantages: (1) it allowed broad conclusions about marine versus terrestrial food utilization by the EHG and MHG; and (2) it constrained the ranges of feasible dietary proportions more than was the case for individual food sources, which aided in interpretation. The reason for the narrower ranges for the aggregate food groups lies in the isotopic similarity of its members. For example, all the marine foods are isotopically enriched in both C and N compared to the terrestrial foods. Thus, in a broad sense, a certain proportion of marine foods must be in the diet to account for the human isotopic signatures, which are intermediate between the terrestrial and marine ends of the spectrum. This marine contribution could come from a variety of combinations of fish, shellfish, and pinnipeds. Individual marine food sources may range all the way from zero contribution to a majority of the marine contribution, but the sum of the three must be in a fairly narrow range to balance the terrestrial contributions in a way that accounts for the observed human isotopic signatures.

7. Sensitivity analysis: terrestrial plant C/N ratios

Often, the most difficult variable to constrain in a paleodietary reconstruction is the relative proportion of various terrestrial plant foods. As demonstrated in Table 3, terrestrial plant C/N ratios vary considerably,
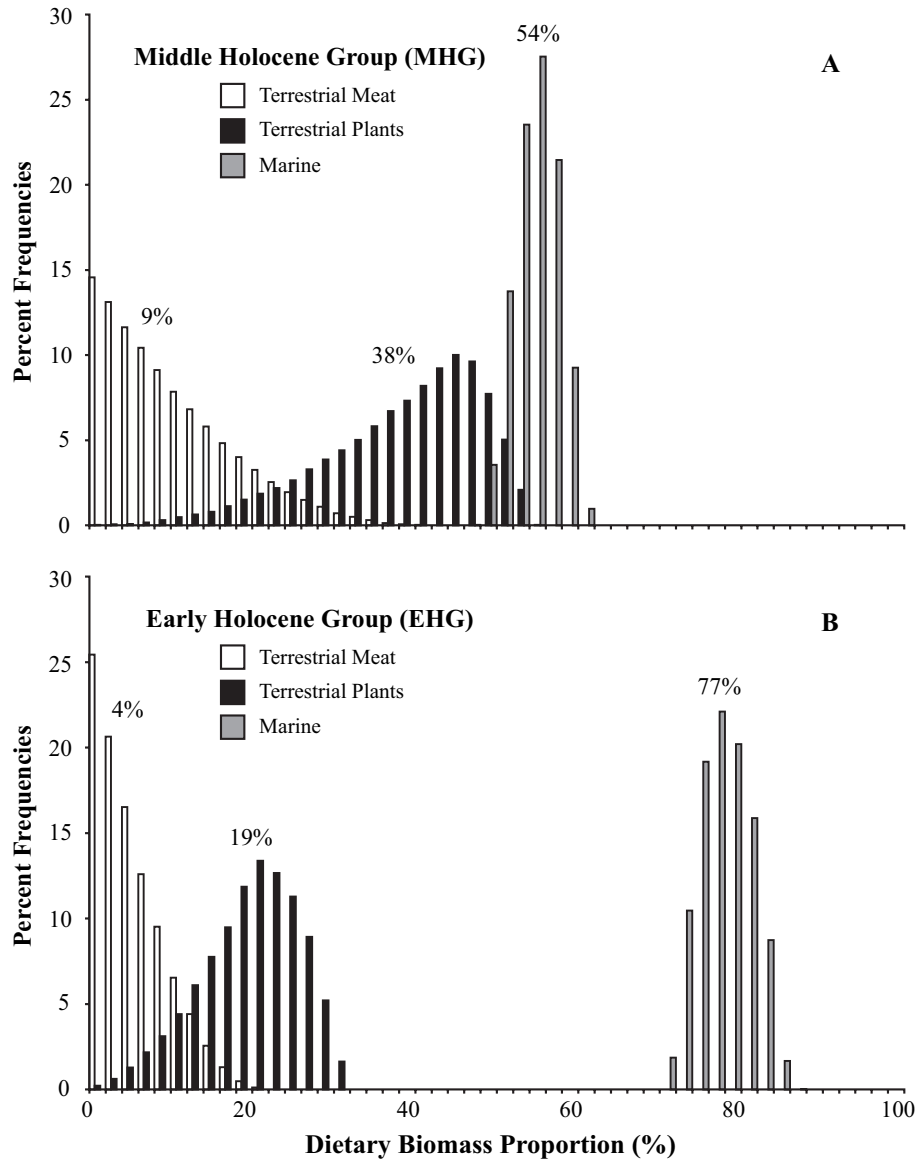
Fig. 3. Dietary biomass proportions of the three aggregate sources for each group. The aggregate solutions are the sum of the biomass contributions for food sources in each category (e.g., the marine aggregate includes data for pinnipeds, shellfish, and marine fish). The aggregate contributions are calculated for all model iterations (in 2% increments), and are expressed as the percent frequency of all possible solutions. The mean proportion of each aggregate distribution is labeled.

depending on the relative concentrations of macromolecular compounds (e.g., protein, lipid, carbohydrate) with different concentrations of carbon. To test the influence of terrestrial plant C/N ratios on other dietary sources, we analyzed the mean biomass proportions of pinnipeds, marine fish, shellfish, terrestrial meat, and terrestrial plants as a function of aggregated plant C/N ratio. For each of the feasible seven-source combinations (11,345 for EHG and 35,021 for MHG) we calculated the aggregated plant C/N ratio as the sum of the biomass proportion times the [C] for each of the three plant types, divided by the sum of the biomass proportion times the [N] for each plant type. This is

essentially the total plant C contribution divided by the total plant N contribution.

Fig. 4 presents the spectrum of mean source contributions for each food source over the range of suitable terrestrial plant C/N ratios. While there is actually a distribution of dietary contribution values for each food source at each plant C/N ratio value, for graphical clarity only the mean values are shown to illustrate the change in central tendency for these distributions in response to plant C/N. The sensitivity analysis shows how the mean proportions of biomass assimilated from each source vary as the [C] of terrestrial plants are changed. Generally, as terrestrial
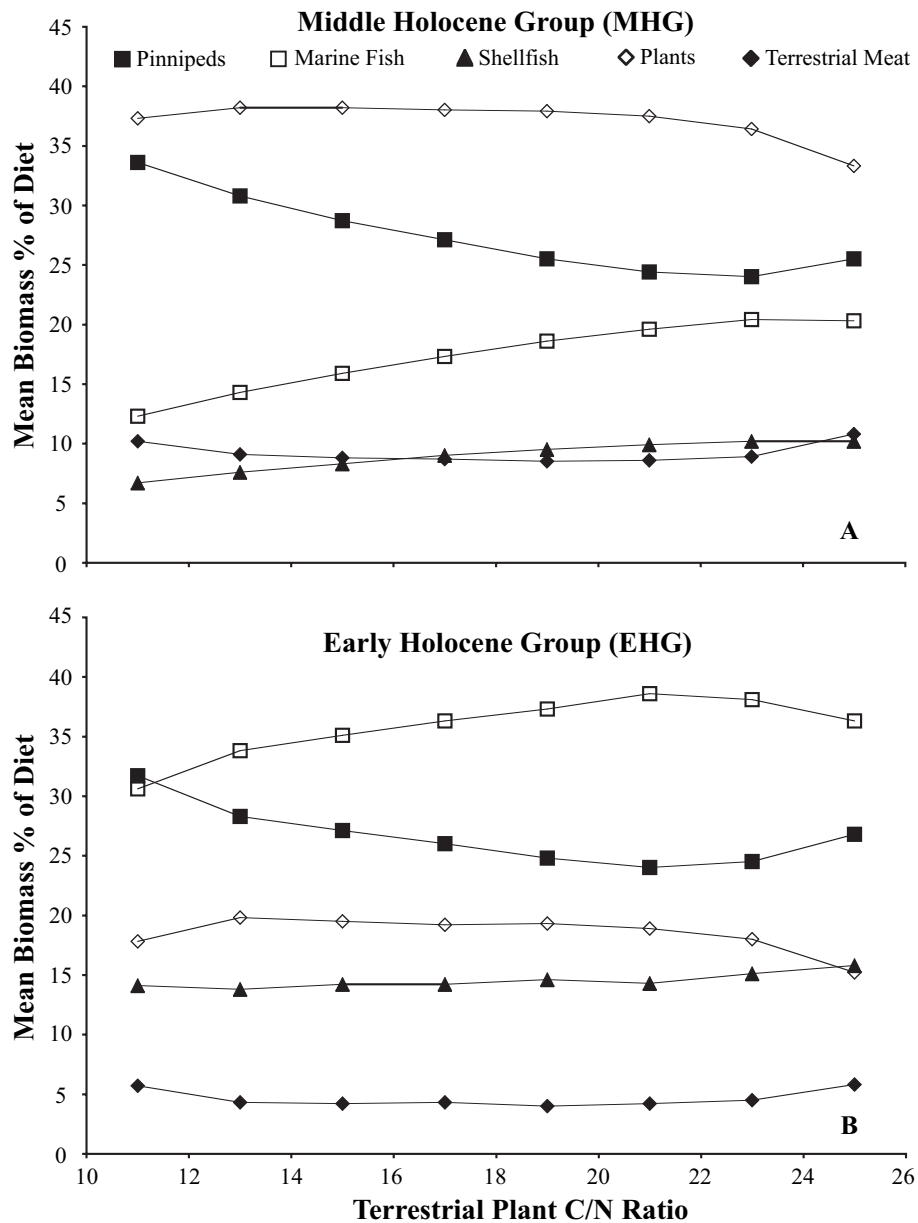
Fig. 4. Terrestrial plant C/N sensitivity analysis for each group using a five-source IsoSource model. The mean proportional value (% of diet) of each food source changes as the C/N ratio for the terrestrial plant source varies from 10 (e.g., leafy plants) to 25 (e.g., nuts).

plant C/N ratios increase, the estimated mean proportion of pinnipeds decreases, with concomitant increases in the mean percentage of shellfish. The largest changes are seen in the mean percentage of pinnipeds, with ∼10% (MHG) to 15% (EHG) decrease in the dietary percentage from the minimum to maximum of plausible terrestrial plant C/N ratios. On the other hand, the largest increase in mean dietary contribution is seen in the percentage of marine fish, with ∼10% increase in both groups with increasing terrestrial plant C/N ratios. The relative mean percentage of the shellfish, terrestrial meat, and terrestrial plant sources stay constant as plant C/N ratios increase. These examples articulate the

importance of considering the elemental concentrations of various sources when utilizing stable isotope mixing models to determine the relative proportion of each source in a diet.

8. Discussion

The dietary data from SCR-60/130 are in agreement with the early Holocene archaeofaunal evidence from southern California implying a relatively early exploitation of marine vertebrates [20,23,53,54,69]. Modeling results suggest a relatively early intensification in marine

resource use, with marine fish (0−68%, mean 36%) and mammals (4−48%, mean 26%) being significant dietary sources for the EHG (Table 4).

Jones [31] presented bone collagen isotopic data for six human burials from the Big Sur coast, ranging in age from 6400 bp to European contact. After accounting for the fractionation values applied to the SCR-60/130 data in this paper, the two individuals from Big Sur that date to the mid-Holocene have considerably lower carbon and nitrogen isotope values (δ^{13}C: −17.9; δ^{15}N: 7.2) than the MHG from SCR-60/130 (δ^{13}C: −16.3; δ^{15}N: 9.5), suggesting that the Big Sur individuals consumed less marine foods than the MHG from SCR-60/130. On the other hand, isotope values of the Big Sur individuals (4) that date from the Late Period (1000−250 bp) are similar to the MHG from SCR-60/130.

Isotopically derived paleodietary reconstructions for prehistoric human populations are also available from southern CA. Walker and DeNiro [73] presented δ^{13}C and δ^{15}N data for human burials from the Santa Barbara Channel region, including individuals from island, mainland, and interior archaeological sites. Using a standard linear isotope mixing model with two 'end-member' food sources (terrestrial and marine mammals), they found a progressive decrease in dependence on marine resources from the Channel Islands to the interior, with mainland coast groups consuming a mixed 65:35 marine-to-terrestrial diet. In addition, isotopic differences between Early (>7000−3400 bp) and Late Periods (1000−200 bp) suggest a substantial increase in the consumption of marine resources over time. This general trend is consistent with archaeofaunal, pathological, and artifactual evidence from the Santa Barbara Channel region of increases in marine resource exploitation during the Late Period [25,34, 72,74]. A temporal comparison between southern CA and the burials from SCR-60/130 is not possible due to the loose temporal constraints reported for southern CA data. For instance, the Santa Barbara Channel Late Period is not represented at SCR-60/130 and the Early Period described in Walker and DeNiro [73] could correlate to either the EHG or MHG from SCR-60/130. However, a direct comparison of carbon and nitrogen isotope values between the groups from SCR-60/130 and those from southern CA reveals that the EHG from central CA is more similar to Channel Island inhabitants than to Santa Barbara Channel mainland coast populations. Unlike prehistoric populations who inhabited the Channel Islands, prehistoric populations living along the central CA coast would have had access to a relatively productive terrestrial landscape. Yet, our results suggest that the early Holocene group from SCR-60/130 were as dependent on marine resources as southern CA island populations. On the other hand, MHG δ^{13}C values suggest a higher dependence on terrestrial resources than coeval mainland groups from

southern CA, but the MHG has a higher mean δ^{15}N value than any of the mainland coast groups from the Santa Barbara Channel. This discrepancy may be in part explained by regional differences in isotope values at the base of the marine and/or terrestrial food webs.

To explain observed shifts in subsistence economies, archaeologists often present ecological hypotheses dependent on external forcing mechanisms, in which changes in terrestrial and/or marine environmental conditions determine the type and abundance of various resources available to prehistoric human populations [26,27]. In such models, paleoclimatic data (offshore sediment cores, terrestrial pollen-based records, climate modeling results) are often used to provide a framework in which to place observed changes in prehistoric subsistence strategies. However, paleoclimatic data sometimes conflict, and only a few high-resolution paleoclimate records exist for central or northern CA. Offshore sediment cores located within the California Current system indicate that sea surface temperatures were slightly cooler (1−2 °C) than present during the middle Holocene from 8000−3000 bp, which might be viewed as evidence for increased upwelling of cold, nutrient-rich water (and presumably increased marine primary production; 5,44,57). On the other hand, more direct measures of marine productivity in offshore settings (relative diatom abundance and opal content) indicate lower productivity than at present from 8000−5000 bp [5]. Regional climate simulations support these later observations, suggesting that the California Current system was characterized by a longer but less intense upwelling season at ∼6000 bp [19]. The relative percentage of coastal redwood (*Sequoia sempervirens*) in both terrestrial and offshore pollen records has also been utilized as an paleo-upwelling proxy, since redwoods are highly dependent on summer fog created by the upwelling of cold water in coastal regions. Pollen-based records show a relatively low percentage of redwood at 8000 bp, with a gradual increase to modern percentages by ∼3500 bp, again suggesting an increase in coastal upwelling intensity over time. Increases in marine productivity presumably would have enhanced the marine resource base available to prehistoric populations living on the coast in the mid-Holocene. However, the EHG from SCR-60/130 has a relatively high marine dietary contribution (70−84%) in comparison to the MHG (48−58%), providing no evidence for an increase in marine resource use over time. The EHG were able to procure a significant amount of marine resources during an interval marked by lower than modern upwelling intensity and marine productivity. This suggests that the EHG was highly adapted to a marine subsistence.

On land, the early to middle Holocene (8000− 5000 bp) was a period of widespread aridity in the western interior of North America (mid-Holocene Altithermal; 4,45,49). In central CA, warmer and drier

conditions on land most likely led to an expansion of oak woodland, chaparral, and grassland habitats [1], resulting in increases in the availability of terrestrial plant resources to prehistoric human populations. Perhaps in response to warmer and drier conditions on land, subsistence models argue for an increase in the procurement of terrestrial plant resources over time, beginning with the appearance of handstones and millingslabs in various regions sometime between 8000 and 5000 bp [21,40,75]. Such ground stone tools are associated with intensive processing of small terrestrial plant resources, suggesting that grass seeds and grains dominated the vegetal component of the diet at this time. The appearance of the mortar and pestle ca. 6000–5500 bp presumably represents a larger investment in processing a wide variety of terrestrial plant and animal resources [9,20,31,32]. In addition, extensive archaeofaunal data suggest that the dietary importance of shellfish decreased and hunted resources (e.g., terrestrial meat, marine fish, pinnipeds) became more important during this interval, as part of a transition from a relatively mobile subsistence strategy focused on selective gathering to a more sedentary lifeway focused on hunting [20,22,31].

The modeling results from SCR-60/130 agree with the general pattern of coastal subsistence strategies described above. The MHG from SCR-60/130 is characterized by a greater consumption of terrestrial plant resources in comparison to the EHG, as shown by increases in the range and mean value of feasible solutions for the aggregate terrestrial plant food source. The distribution for the MHG is centered over a dietary biomass contribution of 38% (range 10–52%), twice the mean value of 19% for the EHG (range 4–30%), with some overlap in the ranges of each distribution (Fig. 3). In addition, the possible ranges of feasible solutions for each terrestrial plant source nearly doubles from the EHG to the MHG (Table 4). Furthermore, possible values for shellfish consumption decrease slightly from the EHG (range 0–36%, mean 14%) to the MHG (range 0–24%, mean 9%), as predicted by subsistence models. The relatively high percentage of pinnipeds in both the EHG (range 4–48%, mean 26%) and MHG (range 6–48%, mean 27%) also conforms to subsistence model predictions, especially after taking into account the relative decrease in marine resource consumption over time. Both the range and mean biomass contribution for the terrestrial meat source also increase from the EHG (range 0–16%, mean 4%) to the MHG (range 0–30%, mean 9%), however, terrestrial meat is a relatively minor dietary source for both groups. On the other hand, the mean biomass contribution of marine fish for the MHG (18%) is half the value of the EHG (36%), conflicting with subsistence model expectations. However, since the

ranges for feasible marine fish diet contributions overlap extensively between the MHG (0–68%) and EHG (0–44%), the lack of change or even an increase in marine fish utilization cannot be ruled out by the isotopic data.

The paleodiet data from SCR-60/130 generally agree with hypotheses regarding the intensification of terrestrial plant processing and consumption from the early to middle Holocene. Overall, the shifts in subsistence at SCR-60/130 suggest that the diets of prehistoric populations from this region were more influenced by changes in terrestrial climate, and presumably increased terrestrial productivity (greater availability of terrestrial plant resources), than shifts in marine productivity. Furthermore, ecologically based hypotheses arguing that an increase in marine productivity throughout the Holocene provided an enlarged resource base to growing human populations may not apply to the central California coast.

9. Conclusions

The SCR-60/130 human burials can be separated into two distinct groups with significant temporal and dietary differences. We conclude: (1) the early Holocene group requires ~75% (70–84%) marine food source contribution, whereas the middle Holocene group requires ~55% (48–58%) marine food source contribution. (2) Pinnipeds were an important marine food source for both groups, so the drop in marine resources likely indicates relatively less marine fish in MHG diets. (3) The dietary contribution of terrestrial plants and/or meat increased over time. (4) Sensitivity analyses demonstrate that C/N ratios of dietary sources can have a considerable control on relative source contributions, and thus are important for accurately modeling ancient diets. Overall, this study demonstrates the utility of a concentration-dependent stable isotope mixing model [47] in an iterative framework [48] to provide feasible ranges of dietary contributions when the number of food sources precludes a unique solution.

Appendix A. Measured isotope values and elemental concentrations of modern pinniped and shellfish samples collected in Monterey Bay

Table 1A
Modern pinniped and shellfish data

	$\delta^{13}C$	$\delta^{15}N$	[C]	[N]	C/N
Pinniped muscle (5)	−17.6	17.8	48.5	13.8	3.5
	(0.7)	(1.2)	(7.1)	(2.0)	(0.1)
Pinniped blubber (5)	−21.6	18.0	72.6	5.0	14.9
(*Zalophus californianus,*	(0.7)	(1.2)	(19.9)	(1.4)	(3.3)
Phoca vitulina, Mirounga					
angustirostris)					
60:40 Muscle-to-	−19.2	17.9	58.1	10.3	5.6
blubber-mixture					
Correction$_{(60:40\ mixture−muscle)}$	−1.6	0.1			
Shellfish (8)	−14.7	9.7	42.6	12.8	3.3
(*Mytilus californianus*)	(0.3)	(0.8)	(1.7)	(1.6)	(0.4)

Pinniped muscle and blubber isotope values were measured to determine a suitable correction (assuming a 60:40 muscle-to-blubber mixture) that was applied to measured isotope values of pinniped archaeofauna from SCR-60/130 (Table 2). Modern pinniped [C] and [N] were measured, and corrected assuming a 60:40 muscle-to-blubber mixture for direct input into the IsoSource model (Table 3). Shellfish isotope values and elemental concentrations were also measured for direct input into IsoSource (Tables 2 and 3). 1‰ was subtracted from shellfish $\delta^{13}C$ values to account for the 'Suess' effect.

References

[1] D.P. Adam, R. Byrne, E. Luther, A Late Pleistocene and Holocene pollen record from Laguna de las Trancas, Northern Coastal Santa Cruz County, California, Madrono 28 (1981) 255–272.

[2] S.H. Ambrose, L. Norr, Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate, in: J.B. Lambert, G. Grupe (Eds.), Prehistoric Human Bone: Archaeology at the Molecular Level, Springer-Verlag, New York, 1993, pp. 1–37.

[3] S.J. Ambrose, Preparation and characterization of bone and tooth collagen from isotopic analysis, Journal of Archaeological Science 17 (1990) 431–451.

[4] D.I. Axelrod, Holocene climatic change in relation to vegetation disjunction and speciation, American Naturalist 117 (1981) 847–870.

[5] J.A. Barron, L. Heusser, T. Herbert, M. Lyle, High-resolution climatic evolution of coastal northern California during the past 16,000 years, Paleoceanography 18 (1) (2003) 1020.

[6] M. Ben-David, D.M. Schell, Mixing models in analyses of diet using multiple stable isotopes: a response, Oecologia 127 (2001) 180–184.

[7] B.R. Bocek, Ethnobotany of Costanoan Indians, California, based on collections by John P. Harrington, Economic Botany 38 (2) (1984) 240–255.

[8] G.S. Breshcini, T. Haversat, Archaeological Evaluation of CA-MNT-234, at the Site of the Proposed Moss Landing Marine Laboratory, Moss Landing, Monterey County, California, Archaeological Consulting, Salinas, CA, 1995.

[9] G.S. Breshcini, T. Haversat, Archaeological investigations at CA-MNT-108, at Fisherman's Wharf, Monterey, Monterey County, California, in: G.S. Breshcini, T. Haversat (Eds.), Archives of California Prehistory, Coyote Press, Salinas, CA, 1989.

[10] T.A. Brown, D.E. Nelson, J.S. Vogel, J.R. Southon, Improved collagen extraction by modified Longin method, Radiocarbon 30 (1988) 171–177.

[11] R.K. Burton, J.J. Snodgrass, D. Gifford-Gonzalez, T. Guilderson, T. Brown, P.L. Koch, Holocene changes in the ecology of northern fur seals: insights from stable isotopes and archaeofauna, Oecologia 128 (1) (2001) 107–115.

[12] R. Cambra, A. Leventhal, L. Jones, J. Hammett, L. Field, N. Sanchez, Archaeological investigations at *Kaphan Umux* (Three Wolves) site, CA-SCL-732: a Middle Period cemetery on Coyote Creek in Southern San Jose, Santa Clara County, California, MS thesis, Oakland, CA, 1996.

[13] B.S. Chisholm, D.E. Nelson, H.P. Schwarcz, Marine and terrestrial protein in prehistoric diets on the British Columbia Coast, Current Anthropology 24 (3) (1983) 396–398.

[14] B.S. Chisholm, H.P. Schwarcz, Stable carbon isotope ratios as a measure of marine versus terrestrial protein in ancient diets, Science 216 (1982) 1131–1132.

[15] C.F. Consolazio, R.E. Johnson, L.J. Pecora, Physiological Measurements of Metabolic Functions in Man, McGraw-Hill, New York, NY, 1963.

[16] J.M. Corum, An examination of intersite variability during the Millingstone Horizon of Southern California, MS thesis, California State University, Northridge, Northridge, CA, 1977.

[17] D.P. Costa, personal communication, University of California-Santa Cruz, 2003.

[18] B. Culleton, T. Jackson, Archaeological Investigations at CA-SCR-60. Pacific Legacy, Inc., Santa Cruz, CA, in preparation.

[19] N.S. Diffenbaugh, L.C. Sloan, M.A. Snyder, Orbital suppression of wind drive upwelling in the California Current at 6ka, Paleoceanography 18 (2) (2003) 1051.

[20] J.M. Erlandson, Early Hunter–Gatherers of the California Coast, Plenum Press, New York, NY, 1994.

[21] J.M. Erlandson, Shellfish and seeds as optimal resources: early Holocene subsistence on the Santa Barbara Coast, in: J.M. Erlandson, R.H. Colten (Eds.), Hunter–Gatherers of Early Holocene Coastal California, Institute of Archaeology, Los Angeles, CA, 1991.

[22] J.M. Erlandson, The role of shellfish in prehistoric economies: a protein perspective, American Antiquity 53 (1) (1988) 102–109.

[23] J.M. Erlandson, T.C. Rick, R.L. Vellanoweth, D.J. Kennett, Marine subsistence at a 9300 year-old shell midden on Santa Rosa Island, California, Journal of Field Archaeology 26 (1999) 255–265.

[24] L.Z. Gannes, C. Martinez del Rio, P.L. Koch, Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology, Comparative Biochemistry and Physiology A 119 (1998) 725–737.

[25] M. Glasgow, Recent developments in the archaeology of the Channel Islands, in: D.M. Power (Ed.), The California Islands, Santa Barbara Museum of Natural History, Santa Barbara, CA, 1980, pp. 79–99.

[26] M. Glasgow, L. Wilcoxon, Coastal adaptation near Point Conception, California, with particular regard to shellfish exploitation, American Antiquity 53 (1988) 36–51.

[27] M.A. Glasgow, D.J. Kennett, J.P. Kennett, L.R. Wilcoxon, Confirmation of middle Holocene ocean cooling inferred from stable isotopic analysis of prehistoric shells from Santa Cruz Island, California, in: W.L. Halverson, G.J. Maender (Eds.), The Fourth California Islands Symposium: Update on the Status of Resources, Santa Barbara Museum of Natural History, Santa Barbara, CA, 1994, pp. 223–232.

[28] K.W. Gobalet, T.L. Jones, Prehistoric Native American fisheries of the Central California Coast, Transactions of the American Fisheries Society 124 (1995) 813–823.

[29] M.G. Hylkema, Prehistoric Native American adaptations along the Central California Coast of San Mateo and Santa Cruz Counties, MS thesis, San Jose State University, San Jose, CA, 1991.

[30] D.A. Jones, W.R. Hildebrandt, Archaeological Excavation at Sand Hill Bluff: Portions of a Prehistoric Site CA-SCR-7, Santa Cruz County, CA, Far Western Anthropological Research Group, Inc., Davis, CA, 1990.

[31] T.L. Jones, Mortars, pestles, and division of labor in prehistoric California: a view from Big Sur, American Antiquity 61 (2) (1996) 243–264.

[32] T.L. Jones, J. Haney, Excavation and Conservation of Six Archaeological Sites at Landels-Hall Big Creek Reserve, Monterey County, California, The Nature Conservancy, San Francisco, CA, 1992.

[33] M.A. Katzenburg, Advances in stable isotope analysis of prehistoric bones, in: S.R. Saunders, M.A. Katzenburg (Eds.), Skeletal Biology of Past Peoples, Wiley-Liss, New York, 1992, pp. 105–119.

[34] C.D. King, The evolution of Chumash society: a comparative study of artifacts used in social system maintenance in the Santa Barbara Channel Region before A.D. 1804, PhD thesis, University of California-Davis, Davis, CA, 1981.

[35] P.L. Koch, Isotopic reconstruction of past continental environments, in: R. Jeanloz, A.L. Albee, K.C. Burke (Eds.), Annual Review of Earth and Planetary Sciences, Annual Reviews, Palo Alto, CA, 1998, pp. 573–613.

[36] P.L. Koch, D.L. Phillips, Incorporating concentration dependence in stable isotope mixing models: a reply to Robbins, Hilderbrand and Farley (2002), Oecologia 133 (2002) 14–18.

[37] H.W. Krueger, C.H. Sullivan, Models for carbon isotope fractionation between diet and bone, in: J.R. Turnland, P.E. Johnson (Eds.), Stable Isotopes in Nutrition, American Chemical Society, Symposium Series, American Chemical Society, Washington, DC, 1984, pp. 205–220.

[38] E.A. Little, M.J. Schoeninger, The late woodland diet on Nantucket Island and the problem of maize in coastal New-England, American Antiquity 60 (2) (1995) 351–368.

[39] R.L. Lyman, Prehistory of the Oregon Coast, Academic Press, San Diego, CA, 1991.

[40] C.W. Meighan, California, in: R.E. Taylor, C.W. Meighan (Eds.), Chronologies in New World Archaeology, Academic Press, New York, NY, 1978, pp. 223–240.

[41] C.W. Meighan, Early shell mound dwellers of the Pacific Coast of North America, in: The Development of Hunting−Fishing−Gathering Maritime Societies on the Pacific, Washington State University Press, Pullman, WA, 1989.

[42] C.W. Meighan, Pacific Coast Archaeology, in: H. Wright, D. Frey (Eds.), The Quaternary of the United States, Princeton University Press, Princeton, NJ, 1965, pp. 709–720.

[43] N.J. van der Merwe, A.C. Roosevelt, J.C. Vogel, Isotopic evidence for prehistoric subsistence change at Parmana, Venezuela, Nature 292 (1981) 536–538.

[44] A.C. Mix, D.C. Lund, N.G. Pisias, P. Boden, L. Bornmalm, M. Lyle, J. Pike, Rapid climate oscillations in the northeast Pacific during the last deglaciation reflect northern and southern hemisphere sources, in: P.U. Clark, R.S. Webb, L.D. Keigwin (Eds.), Mechanisms of Global Climate Change at Millennial Time Scales, American Geophysical Union Monography, 1999, pp. 127–148.

[45] L.J. Mock, A.R. Brunelle-Daines, A modern analogue of western United States summer paleoclimate at 6000 years before present, The Holocene 9 (5) (1999) 541–545.

[46] D.L. Phillips, J.W. Gregg, Uncertainty in source partitioning using stable isotopes, Oecologia 127 (2) (2001) 171–179.

[47] D.L. Phillips, P.L. Koch, Incorporating concentration dependence in stable isotope mixing models, Oecologia 130 (1) (2002) 114–125.

[48] D.L. Phillips, J.W. Gregg, Source partitioning using stable isotopes: coping with too many sources, Oecologia 136 (2) (2003) 261–269.

[49] S.C. Porter, G.H. Denton, Chronology of neoglaciation in the North American cordillera, American Journal of Science 265 (1967) 177–210.

[50] T.D. Price, The Chemistry of Prehistoric Human Bone, Cambridge University Press, Cambridge, UK, 1989.

[51] P.D. Quay, B. Tilbrook, C.S. Wong, Oceanic uptake of fossil fuel CO_2—^{13}C evidence, Science 256 (1992) 74–79.

[52] P.B. Reed, Nutrition: an Applied Science, West Publishing Company, St. Paul, 1980.

[53] T.C. Rick, J.M. Erlandson, Early Holocene fishing strategies on the California Coast: evidence from SBA-2057, Journal of Archaeological Science 27 (2000) 621–633.

[54] T.C. Rick, J.M. Erlandson, R.L. Vellanoweth, Paleocoastal marine fishing on the Pacific Coast of the Americas: perspectives from Daisy Cave, California, American Antiquity 66 (4) (2001) 595–613.

[55] C.T. Robbins, Wildlife Feeding and Nutrition, Academic Press, San Diego, CA, 1993.

[56] K. Roper, Archaeological data recovery excavation at CA-SCR-38/123, Wilder Ranch, Santa Cruz, California, MS thesis, Sonoma State University, Santa Rosa, CA, 1993.

[57] A.L. Sabin, N.G. Pisias, Sea surface temperature changes in the northeastern Pacific Ocean during the past 20,000 years and their relationship to climate change in northwestern North America, Quaternary Research 46 (1) (1996) 48–61.

[58] M.J. Schoeninger, K. Moore, Bone stable isotope studies in archaeology, Journal of World Prehistory 6 (2) (1992) 247–296.

[59] M.J. Schoeninger, M.J. DeNiro, H. Tauber, Stable nitrogen isotope ratios of bone collagen reflect marine and terrestrial components of prehistoric human diet, Science 220 (1983) 1381–1383.

[60] R. Schwaderer, Archaeological test excavation at the Duncan's Point Cave, CA-SON-348/H, in: T.L. Jones (Ed.), Essays on the Prehistory of Maritime California, Center for Archaeological Research, Davis, CA, 1992.

[61] H.P. Schwarcz, Some theoretical aspects of isotope paleodiet studies, Journal of Archaeological Science 18 (1991) 261–276.

[62] R.E. Sonnerup, P.D. Quay, A.P. McNichol, J.L. Bullister, T.A. Westby, H.L. Anderson, Reconstructing the oceanic C-13 Suess effect, Global Biogeochemical Cycles 13 (4) (1999) 857–872.

[63] M.J. Stenhouse, M.S. Baxter, Bomb ^{14}C and human radiation burden, Nature 267 (1977) 825–827.

[64] M. Stuiver, P.J. Reimer, Extended ^{14}C data base and revised Calib 3.0 ^{14}C Age Calibration Program, Radiocarbon 35 (1993) 215–230.

[65] M. Stuiver, P.J. Reimer, Calib 4.0 Radiocarbon Calibration Program, Quaternary Isotope Lab, University of Washington, Seattle, WA, 1998.

[66] L.L. Tieszen, T.W. Boutton, K.G. Tesdahl, N.A. Slade, Fractionation and turnover of stable carbon isotopes in animal tissues: implications for the $\delta^{13}C$ analysis of diet, Oecologia 57 (1983) 32–37.

[67] A.K. Toperoff, Diet of harbor porpoise (*P. phocoena*) using stomach contents and stable isotope analyses, MS thesis, CSU-Monterey Bay, Moss Landing, CA, 2001.

[68] USDA, USDA Nutrient Database, U.S. Department of Agriculture, http://www.nal.usda.gov/fnic/foodcomp/, 2003.

[69] R.L. Vellanoweth, M.R. Lambright, J.M. Erlandson, T.C. Rick, Early New World maritime technologies: sea grass cordage, shell beads, and a bone tool from Cave of the Chimneys, San Miguel Island, California, USA, Journal of Archaeological Science 30 (2003) 1161–1173.

[70] J.C. Vogel, N.J. van der Merwe, Isotopic evidence for early maize cultivation in New York State, American Antiquity 42 (1977) 238–242.

[71] T.A. Wake, D.D. Simons, Trans-Holocene Subsistence strategies and topographic change on the Northern California Coast: the fauna from Duncan's Point Cave, Journal of California and Great Basin Anthropology 22 (2) (2000) 295–320.

[72] P.L. Walker, J.M. Erlandson, Dental evidence for prehistoric dietary change on the northern Channel Islands, American Antiquity 51 (1986) 375–383.

[73] P.L. Walker, M.J. DeNiro, Stable nitrogen and carbon isotope ration in bone collagen as indices of prehistoric dietary dependence on marine and terrestrial resources in Southern California, American Journal of Physical Anthropology 71 (1986) 51–61.

[74] P.L. Walker, P. Snethkamp, Archaeological investigations on San Miguel Island: archaeological and physical anthropological research, National Park Service, Western Region, San Francisco, CA, 1984.

[75] W. Wallace, in: R.F. Heizer (Ed.), Post-Pleistocene Archaeology, 9000 to 2000 B.C., Smithsonian Institution, Washington, D.C., 1978, pp. 25–36.