



Early specialized maritime and maize economies on the north coast of Peru

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We assess diet and economies of middle Holocene (~7,500 to 4,000 calibrated [cal] B.P.) humans at coexisting mound sites (Huaca Prieta and Paredones) in north coastal Peru and document regular consumption of maize by ~6,500 to 6,000 cal B.P. and its earliest use as a staple food in this area of the Andes between 5,000 and 4,500 cal B.P. Stable isotope data from enamel carbonates and dentin collagen (childhood diet) and dental microwear texture analysis (adult diet) demonstrate dietary and economic specialization. Previous studies revealed maize and mixed-food refuse at both sites, but this study documents actual food consumption, showing that these communities situated a few hundred meters apart had significantly distinct diets in childhood and adulthood. Huaca Prieta focused on marine resources, although there are some contributions from terrestrial meat. Paredones individuals primarily consumed maize during childhood (up to 70% of the juvenile diet), as shown by $\delta^{13}\text{C}$ values, apatite-collagen spacing, and discriminant analysis of $\delta^{13}\text{C}_{\text{coll}}$, $\delta^{13}\text{C}_{\text{carb}}$, and $\delta^{15}\text{N}$ values. Maize was likely used as a weaning food (e.g., gruel and/or *chicha*—a maize beverage), hinting at the significant role of breastfeeding mothers, weaning infants, and children in the development of maize as a staple crop. Additionally, dental microwear data show Paredones adult diets are high in abrasives, potentially from maize processing. The distinct foodways at these neighboring sites result from and also reflect their social and political distinctions. These differences in food production, distribution, and consumption generated opportunities for exchange, an interaction that bound them together in mutual benefit.

stable isotopes | Andes | diet | dental microwear | maize

The Andes of South America is one of only a few regions in the world where the independent development of proto-urbanism, political hierarchy, and variable strategies of food production occurred. The area produced a wide variety of crops, including potato, corn, bean, peanut, chili pepper, avocado, tomato, quinoa, cotton, and others (1–4). Furthermore, the offshore waters of the Pacific coast from Ecuador to Chile provide some of the most diverse and abundant marine resources in the world due to the cold Humboldt Current and major upwelling (5). Archaeological research along the coast has revealed some of the most elaborate Preceramic maritime societies, including the Chinchorro culture of southern Peru and northern Chile dated between at least ~7,500 and 4,500 y ago (6, 7) and the slightly later Preceramic mound cultures from southern Ecuador to central Peru that subsisted on both seafood and farming (8–11). The Central Andes, especially coastal Peru, is the most notable area in the world where maritime, agricultural, and pastoral economies eventually coalesced to produce early social complexity and later preindustrial states and urbanism with various forms of sociopolitical organization (12, 13).

Although historical documents suggest that late pre-Hispanic communities were typically organized by occupational specialty, such as fishing communities on the coast, farmers in valley bottoms and mountain slopes, and herders in the high altitude

(14–17), the extent and temporal depth of this form of political and socioeconomic organization in the Andes is not well known. Scholars have been debating the veracity of those maritime and other economic specialization models, noting that indigenous elites, particularly from coastal groups, may have presented self-interested characterizations to Spanish administrators, downplaying their precontact agricultural production to minimize tribute demands (18). Scrutinizing those sources and analyzing archaeological data that speak to precontact economic models also provide windows into clarifying other aspects of indigenous sociopolitical systems and practices. For example, occupational specialties intersect with other aspects of community organization, as when communities were comprised of distinct (biological) kinship groups—shaped by occupation—with some intermarrying, forming groups of biological and affinal kinship networks. Scholars suggest that maritime communities were particularly specialized, engaging in fishing, hunting sea lions, and collecting seaweed, shellfish, and marshy plants, activities that required specialized tools, sea craft, and deep knowledge of coastal, littoral, and ocean ecologies (15). Agricultural and pastoral lifeways similarly required specific tools and deep knowledge of local landscapes, ecologies, and other life forms (i.e., plant and animal life). However, these specializations need not preclude other productive capacities; there were exceptions to late pre-Hispanic occupational divisions (19, 20). Furthermore, fishing populations were not always spatially isolated from

Significance

The manner in which early human populations in the Americas organized their subsistence strategies and exchange have profound implications on their socioeconomic organization. Analysis of two coexisting Preceramic communities in coastal Peru (~7,500 to 4,000 calibrated [cal] B.P.) shows that despite their proximity, they ate distinct foods. Huaca Prieta focused on marine resources, Paredones on maize and other crops. They exchanged food items, indicating early forms of cooperation among specialized Preceramic groups. Paredones shows regular maize consumption by 6,500 to 6,000 cal B.P. and maize as a staple by 5,000 to 4,500 cal B.P., particularly as a weaning food. Research on ancient political economies should incorporate isotopic and dental microwear texture data to reveal actual food consumption of the people.

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other occupational groups (21, 22). Whether these groups coresided or lived separately, communities exchanged products to varying degrees, tying them together in varied bonds of reciprocity informed by resource sharing and other forms of cooperation. This occupational specialization also extended into other forms of difference. For example, maritime specialists often used their own types of pottery (22), worshipped their own gods and *huacas*, used different artistic symbols, and identity markers, and, in some cases, spoke their own dialects (15, 23).

In contrast to the occupationally distinct communities that relied on exchange, other scholars have noted that some Andean communities were self-reliant, producing and procuring their own diverse food resources and other goods (e.g., wool and cotton for textiles). The vertical and horizontal archipelago models (24, 25) required that communities acquire and manage territories in distinct ecozones. These self-reliance models that minimized exchange and trade networks, however, required dispersed management of land and resources, as colonists were required to stake claim (or share) certain territories in far flung regions. This form of economic organization also shaped, and was influenced by, sociopolitical dynamics, for example, when marriages were forged to establish claims in a distant zone, effectively diversifying access to food and other resources, such as camelid wool, salt, and obsidian, among other items.

These models are not mutually exclusive, of course, and the varying and overlapping manner in which communities organized themselves to acquire food and other resources is a compelling question to explore (26). Recently, scholars have tackled this issue regarding maritime activities in the Andes, exploring the lifeways and economic and sociopolitical organization of coastal communities from 14,000 y ago to the colonial era (16). Of particular interest here, Prieto (19) details the scholarly history of maritime communities, noting that authors have suggested there was focused marine exploitation in the Late Preceramic and Initial period, which later gave way to more diverse resource exploitation. There are exceptions (19, 20), as when Bird (27) suggested that the early inhabitants of Huaca Prieta (~7,500 to 4,000 calibrated [cal] B.P.) were fishers who engaged in a limited form of farming, and Dillehay (28) presented evidence for the merging of fishing and farming/foraging economies (and cultivating wetlands) that tied communities together and produced novel sociopolitical formations, systems of food production, and community ontologies. Moreover, at the coastal Initial Period (~3,500 to 3,200 cal B.P.) site of Gramalote (~25 km south of Huaca Prieta), where marine resources were an essential component of diets, there is also macro- and microbotanical evidence for limited, local production of agricultural items, such as squash, beans, and chili peppers (19). Gramalote fisherfolk also produced brown cotton for fishing nets and lines, a productive capacity that ensured their autonomy, even as they obtained other farmed foods (e.g., manioc, fruits, and peanuts) from inland groups—a system that may have tied communities together in exchange systems (19, 29).

This study builds on that previous scholarship and adds an essential dimension. We present stable isotope and dental microwear texture data that reveal the actual consumption of certain categories of foods by individual people. Although plant and animal remains and food production tools are crucial for reconstructing what could be on the menu, stable isotope and dental microwear texture data show what people ate and, in doing so, provide deeper insights into understanding economic and resource specialization, mixed economies, and regional political-economic systems. What were the food consumption patterns of Preceramic peoples in north, coastal Peru? What does that reveal about some of the earliest forms of economic specialization and sociopolitical organization among those early groups? When does maize become a staple food, in what form was it consumed, and what are the implications of intense

production and management of this new staple crop in northern Peru? In Mesoamerica, recent stable isotope data show significant maize consumption by 4,700 to 4,000 cal B.P. and maize as a staple food after 4,000 cal B.P. (30). Here, we demonstrate an earlier use of maize as a substantial food source and show its use as a staple food among juveniles on the north coast of Peru by ~5,000 to 4,500 cal B.P.

Previous studies have shown distinct faunal (31) and botanical remains (32, 33) and food-processing artifacts at Paredones and Huaca Prieta, where both mounds changed from being domestic forager locales to food-preparation and ritual sites, respectively (34). However, it is unclear what foods the children and adults were actually eating at each mound site. Did each community procure and produce different foods and then equitably share those resources, or was distinct food production followed by distinct food-consumption practices?

Distinct diets between the two groups would suggest that occupational specialization as related to food procurement (e.g., marine resource extraction vs. agricultural production) and consumption was a key principle of socioeconomic organization in Preceramic times on the north Peruvian coast. In contrast, homogeneity in diets between the two communities could be interpreted in two ways: 1) support for the verticality model, showing that each community procured and produced their own food resources (e.g., marine, agricultural, and wild plant foods), leading to similar diets; or 2) each group specialized in one form of food production (e.g., marine vs. agricultural) but then exchanged extensively, creating similar diets between the two mound groups. As the isotope and dental microwear data will show, the Huaca Prieta and Paredones communities consumed distinct diets, both as children and as adults (with some limited exchange), demonstrating that occupational specialization was a key factor in structuring socioeconomic organization among early Andean populations in this coastal area, a practice that continued—although perhaps intermittently and variably—until Spanish contact (16). In short, while we focus on the empirical data that allow us to reconstruct foods consumed by Preceramic people at Huaca Prieta and Paredones, these data are synthesized with previous research on food production and site use (28, 35, 36) to clarify various aspects of political, social, and economic structures at one of the earliest coastal communities in the Americas.

Regional and Site Background of Huaca Prieta and Paredones

On the north coast of Peru in the lower Chicama Valley, archaeological evidence shows the development of early complexity, where the roughly contemporary Huaca Prieta and Paredones earthen mounds and several nearby Preceramic domestic sites are located across multiple, closely juxtaposed maritime and terrestrial biozones (37, 38) (Fig. 1 and *SI Appendix, Fig. S1*). The Huaca Prieta mound is one of the longest human-occupied sites in the world, spanning more than 14,000 y (36). It was first occupied intermittently by maritime foragers between ~14,500 and 8,500 cal B.P., permanently used with adjacent and distinct residential areas as a ritual and mortuary site between ~7,500 and 4,000 cal B.P. (38), and occasionally afterward from the ceramic to colonial periods as a cemetery (38, 39).

Initial work indicated a primary marine economy mixed with secondary incipient gardening at Huaca Prieta (27, 37, 39). The earliest excavations found plants including squash, chili peppers, beans, achira (*Canna*), bottle gourds, and cotton, suggesting cultivation of these plants and evidence of some of the earliest farmers in the Americas (27). However, Bird and coworkers report they found no Preceramic maize in their 1940s excavations (27, 37, 40). Recent research at Huaca Prieta and Paredones (28) reveals an integrated economy based on at least two distinct social segments of the littoral population with increased

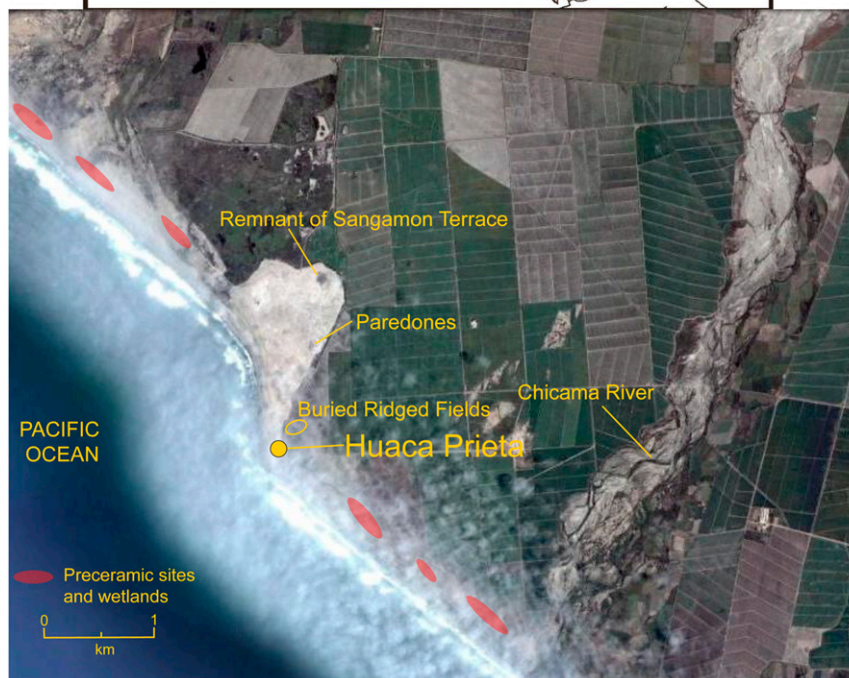


Fig. 1. (Upper) Map showing location of Huaca Prieta mound in northern Peru. (Lower) Location of the Huaca Prieta and Paredones mounds in northern coastal Peru and their proximity to one another (map data from Google Earth).

economic specialization and complementarity between maritime foraging/fishing and agriculture by at least ~9,000 cal B.P. Specialization at these sites also appears to have been related not only to marine and farming practices but also to task or occupational specialization, with some groups or individuals focused on specific resources (i.e., salt production, fish as opposed to shellfish) or resource zones (e.g., estuarine wetlands, shoreline, sea, nearby Andean mountains), and to resource exchanges among ecologically and economically intermixed groups. We do not know if the dual economic specialization, and the ecological diversification it implies, led to increased social differentiation. There is no weaponry or human skeletal trauma (41) to suggest conflict between social groups, although there may have been intergroup competition.

In close proximity to Huaca Prieta (Fig. 1), Paredones has provided some of the earliest evidence in the region of maize production through the presence of cobs, husks, stalks, grains,

and tassels (33). Additionally, different races of Preceramic maize cobs were discovered at Paredones and Huaca Prieta, while phytolith and starch grain evidence of *Zea mays* was documented from artifacts at Paredones (33). Husks and shanks were dated to 6,734 to 6,569 cal B.P. (2 sigma, Southern Hemisphere calibration [SHcal]), suggesting early consumption of maize resources; however, it is unknown whether maize was regularly consumed before 5,000 to 4,500 cal B.P., as maize macrofossils and microfossils and heavy-duty grinding stones are scarce and discontinuous prior to this time (33). While plant macro- and microfossil evidence are critical to dietary interpretations, additional proxies including stable isotope and dental microwear texture analysis (DMTA) can help clarify human diets (e.g., the degree to which maize was consumed and in what age phase of the life course). The human remains examined here span Phases III to IV at Huaca Prieta and Paredones. (See *SI Appendix* for site descriptions and context.)

Huaca Prieta and Paredones were in close proximity to the shoreline at the time of site use (100 and 400 m, respectively), and, thus, each could have provisioned and consumed marine resources on their own, or they could have engaged in economic specialization—as the fauna and botanical data suggest—and then either exchanged those items or kept them for isolated community consumption. We examine these possibilities through analysis of stable carbon- and nitrogen isotope ratios from dentin collagen and stable carbon isotope ratios from enamel carbonates from 21 individuals at Huaca Prieta and 9 individuals from Paredones (*Materials and Methods* and *SI Appendix*). Those data provide a view of childhood diets and allow us to detect similarities and differences in protein and carbohydrate/lipid consumption, owing to their differential routing to respective tissues (42–44). Stable isotope data are also obtained from two faunal specimens from Paredones to begin documenting comparative isotope values from potential animal food sources. Additionally, the textural properties of foods consumed are examined through DMTA of teeth from 20 individuals from Huaca Prieta and 7 individuals from Paredones. Given the different levels of abrasives that typically result from food processing (i.e., grinding maize on sedimentary stone slabs [e.g., limestone]) (45), agriculturalists should exhibit higher abrasion on teeth relative to people primarily reliant on less-grainy marine resources (46). Finally, stable oxygen isotope ratios from enamel carbonates are used to establish whether the individuals are from the same, local geographic region where they were buried. This helps to independently confirm that dietary differences are not the result of nonlocal peoples being interred in the mounds. Together, these data aid in assessing whether each group procured and processed specific food types and then shared them equally or whether distinct food production also meant distinct food consumption by each mound group.

Results

Dietary Stable Isotope Analyses: Animals and Humans. Primary and summarized data are presented in Table 1, Fig. 2, and *SI Appendix, Tables S1 and S2*. Stable carbon isotope values from Paredones individuals ($\delta^{13}\text{C}_{\text{VPDB enamel carbonate}}$ and $\delta^{13}\text{C}_{\text{VPDB dentin collagen}}$; VPDB, Vienna Pee Dee Belemnite) are significantly greater than Huaca Prieta individuals ($P < 0.0001$ and $P < 0.0001$, respectively; Student's t test; *SI Appendix, Table S1*), indicating that Paredones children consumed more ^{13}C -enriched foods (e.g., maize) than Huaca Prieta children. Stable nitrogen isotope values of dentin collagen from the two sites are statistically similar ($P = 0.128$; Student's t test; *SI Appendix, Table S1*).

Documenting the carbonate-collagen spacing in $\delta^{13}\text{C}$ values (48) shows that Huaca Prieta individuals have $\Delta^{13}\text{C}_{\text{enamel carbonate-dentin collagen}}$ values that range from 0.6 to 3.9‰ with a mean of 2.2‰ (SD: 1). This suggests a diet of marine protein and C_3 carbohydrates (i.e., nonmaize plants). In contrast, Paredones individuals have significantly higher $\Delta^{13}\text{C}_{\text{enamel carbonate-dentin collagen}}$ values relative to Huaca Prieta ($P = 0.006$; Student's t test), with an average of 3.9‰ (SD: 1.3). However, half of the Paredones individuals show a $\Delta^{13}\text{C}_{\text{enamel carbonate-dentin collagen}} > 4.4‰$, and the other half are $< 4.4‰$ (s). This would suggest that among those sampled for both tissues, half had a childhood diet of marine protein and C_3 carbohydrates (i.e., nonmaize plants) and half had a diet of C_3 protein and C_4 carbohydrates (e.g., maize and possibly amaranth). However, this carbonate-collagen spacing model was developed with human samples from the Marianas archipelago (48), which may not be wholly appropriate in this South American setting, so we also analyzed the data with two additional models that draw from a greater diversity of archaeological populations and animal studies (49, 50). The results from all three models discussed in the *Results* (excluding Table 1), *Discussion*, and *Conclusion: Effects of Dietary Practices on Economies and Lifestyles* include the 2.3‰

correction to the $\delta^{13}\text{C}_{\text{enamel carbonates}}$ (47), and *SI Appendix* also presents uncorrected results.

Results from the model developed by Kellner and Schoeninger (49) show the two populations in different ends of the graph, revealing the distinctive whole-diet sources of each community (*SI Appendix, Fig. S4*). Huaca Prieta children regularly consumed C_3 energy sources (e.g., nonmaize plants) and Paredones children ate primarily C_4 energy sources. The Huaca Prieta children are close to the marine protein line, but half are between the marine and C_3 protein lines, suggesting some minor consumption of terrestrial meat at least for some. Paredones children are between the C_4 and marine protein line, further clarifying the distinct protein sources between the two communities. The model by Froehle et al. (50) similarly shows the two sites in distinct clusters (Fig. 3). Huaca Prieta is in and near Cluster 1 (100% C_3 plant foods) and trending toward Cluster 3 (marine diets), and Paredones is in and near Cluster 2 (70% C_4 plants; implications are discussed below in *Discussion*). Overall, the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and the assessment of the data against the three models reveal distinct dietary regimes at the two sites, and this is the case whether the $\delta^{13}\text{C}$ values from enamel carbonates are adjusted or not (*SI Appendix*).

Stable Oxygen Isotope Analyses. We analyzed three water samples to obtain the local/regional $\delta^{18}\text{O}_{\text{dw-VSMOW}}$ baseline values (dw-VSMOW, drinking water–Vienna Standard Mean Ocean Water). The $\delta^{18}\text{O}_{\text{dw-VSMOW}}$ from Zaña River and tap water in Chiclayo (~110 km north of Huaca Prieta) both equal $-8.2‰$, and $\delta^{18}\text{O}_{\text{dw-VSMOW}}$ from Trujillo (~25 km south) tap water is $-11.9‰_{\text{dw-VSMOW}}$ (*SI Appendix, Table S1*).

Stable oxygen isotope data from human enamel carbonates are summarized in Table 1 and *SI Appendix, Table S1*. Paredones individuals exhibit $\delta^{18}\text{O}_{\text{enamel VSMOW}}$ ranging from 25.1 to 26.5‰; there is only one statistical outlier (25.1‰), but that sample value is still less than the minimum meaningful difference (MMD), at least as noted for bone apatite (51). The $\delta^{18}\text{O}_{\text{VSMOW}}$ from Huaca Prieta individuals range from 25.3 to 27.7‰. Although stable oxygen isotope values ($\delta^{18}\text{O}_{\text{enamel VSMOW}}$) from Paredones individuals (mean \pm SD: 26.0 ± 0.4) are significantly lower than Huaca Prieta individuals (mean \pm SD: 26.8 ± 0.7 ; $P = 0.003$; z score = 2.964; Mann–Whitney test), the variability of $\delta^{18}\text{O}_{\text{enamel}}$ values are not different between the two populations ($P = 0.068$; Levene's median test). Furthermore, the average difference between the two populations (i.e., less than 1‰) does not exceed the MMD (as established for bone carbonates) (51); thus, there are no data indicating that nonlocals are present among the individuals sampled. Instead, the small range of $\delta^{18}\text{O}_{\text{enamel VSMOW}}$ values suggests that both groups consumed similar local water sources as children.

DMTA. All DMTA data are in Fig. 5 and *SI Appendix, Table S2*. All DMTA variables assessed (i.e., anisotropy [$epLsar$], complexity [$Asfc$], and texture fill volume [Tfv]; *Materials and Methods*) yielded statistical differences between Huaca Prieta and Paredones and prehistoric/historic populations (Fig. 5 and *SI Appendix, Table S2*); DMTA attribute of complexity was the most revealing. Huaca Prieta individuals had complexity values indistinguishable from maritime Fuegians from Tierra del Fuego and significantly lower than all other populations (i.e., Chumash, Khoe-San, Andamanese, and Tigara, listed in order of ascending mean complexity value; $P < 0.05$; Fig. 5). In contrast, Paredones individuals had significantly higher complexity values than Huaca Prieta individuals ($P = 0.037$) and Fuegians, while they had significantly lower values than the Andamanese of the Indian Ocean (and indistinguishable from other global populations such as the Chumash, Khoe-San, and Tigara populations) (Fig. 5).

Tfv values from Huaca Prieta cluster with the Fuegians and Chumash and are statistically indistinguishable from the Tigara

Table 1. Descriptive statistics of stable isotope values from all human individuals sampled from Huaca Prieta and Paredones mounds and two faunal remains (camelid and deer) from Paredones

Mound	Isotope or isotope spacing	N	Min., ‰	Max., ‰	Range, ‰	Median, ‰	Mean, ‰	SD, ‰
Huaca Prieta	$\delta^{13}\text{C}_{\text{enamel carbonate}}$ (VPDB)	21	-14.0	-10.8	3.2	-12.5	-12.4	0.8
	$\delta^{13}\text{C}_{\text{dentin collagen}}$ (VPDB)	13	-18.3	-15.4	2.9	-16.5	-16.7*	1.1
	$\Delta^{13}\text{C}_{\text{carbonate-dentin collagen}}$ (VPDB)	13	2.9	6.2	3.3	4.5	4.4	1.0
	$\delta^{15}\text{N}_{\text{dentin collagen}}$ (AIR)	13	11.4	16.5	5.1	14.7	14.2	1.6
	$\delta^{18}\text{O}_{\text{enamel carbonate}}$ (VSMOW)	21	25.3	27.7	2.4	27.0	26.8	0.7
Paredones	$\delta^{13}\text{C}_{\text{enamel carbonate}}$ (VPDB)	9	-7.0	-3.0	4.0	-4.0	-4.3	1.4
	$\delta^{13}\text{C}_{\text{dentin collagen}}$ (VPDB)	6	-12.6	-10.0	2.6	-10.6	-10.8	1.0
	$\Delta^{13}\text{C}_{\text{carbonate-dentin collagen}}$ (VPDB)	6	3.8	7.4	3.6	6.5	6.2	1.3
	$\delta^{15}\text{N}_{\text{dentin collagen}}$ (AIR)	6	10.2	15.0	4.8	13.0	12.8	2.1
	$\delta^{18}\text{O}_{\text{enamel carbonate}}$ (VSMOW)	9	25.1	26.5	1.4	26.1	26.0	0.4
	Fauna $\delta^{13}\text{C}_{\text{bone collagen}}$ (VPDB)	2	-22.2	-21.5	0.7	-21.9	-21.9	0.7
	Fauna $\delta^{15}\text{N}_{\text{bone collagen}}$ (AIR)	2	4.4	5.3	0.9	4.9	4.9	0.6

Max., maximum; Min., minimum; N, number of specimens sampled; SD, SD ($n - 1$). These statistics are based on raw data (no adjustments were used here). *If the two Huaca Prieta samples with atomic C:N of 2.6 are removed, the $\delta^{13}\text{C}_{\text{dentin collagen}}$ mean is 16.4 (SD: 0.9) and the $\delta^{15}\text{N}_{\text{dentin collagen}}$ mean is 14.7‰ (SD: 1.1).

($P = 0.015$; Fig. 5). Paredones individuals are indistinguishable in *Tfv* from all populations examined, including Huaca Prieta (*SI Appendix, Table S2*); *epLsar* only distinguishes Fuegians from all other populations (including Huaca Prieta but excluding Paredones; $P < 0.05$, Fig. 5 and *SI Appendix, Table S2*). Paredones, in contrast, has higher anisotropy values than Andamanese, Chumash, and Khoe-San ($P < 0.05$; Fig. 5). While it was not possible to chronologically compare DMTA attribute values in the Paredones sample due to limited sample size, Phase III and Phase IV individuals from Huaca Prieta were indistinguishable in *Asfc*, *epLsar*, and *Tfv* (Mann-Whitney *U*: $P = 0.649$, $P = 0.057$, and $P = 0.095$, respectively).

Discussion

Distinct Diets at Huaca Prieta and Paredones. The stable isotope and dental microwear data show distinct dietary regimes. Huaca Prieta individuals were part of a marine economy, although there was some variation in access to marine and terrestrial resources (Figs. 2 and 3 and *SI Appendix, Fig. S3*). The Huaca Prieta DMTA data, which are similar to marine-economy Fuegians, show a strong reliance on soft foods, consistent with the consumption of marine resources that were not processed on sandy beaches (46). Paredones individuals, in contrast, exhibit diets consistent with agricultural economies, consuming primarily maize and terrestrial meat (e.g., deer and camelids) (31) combined with marine inputs and other ^{13}C -enriched proteins. Reliance on maize during childhood is evident from $\delta^{13}\text{C}$ values from enamel carbonate and dentin collagen, and this maize focus continues as adults; they show more pitted teeth (i.e., higher complexity), which likely resulted from processing maize on grinding stones (52).

Stable nitrogen isotope ($\delta^{15}\text{N}_{\text{AIR dentin collagen}}$; AIR, atmospheric nitrogen) values from Huaca Prieta humans (mean $\delta^{15}\text{N}$: 14.7‰) (Table 1 and *SI Appendix, Table S1*) suggest that marine foods were a key aspect of juvenile diets. Comparing Huaca Prieta to other Pacific groups from South America reveals its similarities to marine based economies. For example, at the Middle Horizon (1,400 to 1,000 y ago) coastal fishing community of Ancon, ~35 km north of Lima, the mean $\delta^{15}\text{N}_{\text{AIR bone collagen}}$ is 14.1‰ (53) (statistically similar; Student's *t* test; $P = 0.82$), and coastal populations from Tierra del Fuego with known marine diets exhibit a mean $\delta^{15}\text{N}_{\text{AIR dentin collagen}}$ of 14.8‰ (statistically similar; $U = 80$; z score = 0.5095; $P = 0.61$). While marine foods were prominent at Huaca Prieta, they did not dominate diets to the extent that was found at the Late Intermediate period (1,000 to 600 y ago) coastal sites of Armatambo near Lima and San Geronimo in far southern Peru, where mean $\delta^{15}\text{N}_{\text{AIR bone collagen}}$

is 16.2‰ (54) and 20.9‰ (55), respectively. Both sites show statistically different $\delta^{15}\text{N}$ values relative to Huaca Prieta (Student's *t* test; $P = 0.002$ and $P < 0.0001$, respectively). (See *SI Appendix, Fig. S5* for comparisons to other precontact Andean communities.) Other precontact Pacific coast groups, such as early and middle Holocene populations from central, coastal California, have mean $\delta^{15}\text{N}_{\text{AIR bone collagen}}$ values of 13.6 and 12.5‰, respectively, which suggest 70 to 84% marine food source contributions during the early Holocene and 48 to 58% during the middle Holocene (56). More broadly, historic populations such as the Inuit, Haida, and Tlingit with primarily marine diets have $\delta^{15}\text{N}_{\text{bone collagen}}$ values ranging from 17 to 20‰, while agriculturalists with $\delta^{15}\text{N}$ values between 6 and 12‰ consume primarily terrestrial protein (57). In all, the comparative data help to illustrate the common—although not exclusive—consumption of marine foods in Huaca Prieta diets.

While a discussion of nitrogen isotope values provides a starting point for reconstructing dietary regimes, elevated $\delta^{15}\text{N}$ can be caused by a variety of other reasons, such as extended starvation (58), pathological conditions that affect bone (59), and the consumption of breastmilk (60), while pregnancy can lead to lower $\delta^{15}\text{N}$ values (61). As such, we incorporated other lines of evidence and dietary models to interpret the stable isotope data.

The stable isotope data from the camelid and deer show no evidence that they foraged on C_4 plants, such as maize (Table 1). Although the faunal sample size is small, this tentatively suggests that the consumption of these terrestrial animals would not elevate the $\delta^{13}\text{C}$ values of humans.

Dental microwear texture data and the presence of auditory exostoses further clarify the role of a primarily marine-based economy at Huaca Prieta. Microwear data show low complexity values (Fig. 5), which is consistent with a diet characterized by the immediate consumption of marine meat, in contrast to populations that prepare their food on sandy beaches, which picks up abrasives. Auditory exostoses—bony growths in the external auditory meatus (ear canal)—are skeletal evidence of swimming and diving in water (62), especially cold water (63). They are present on 86% of Pre-ceramic adult males ($n = 7$) and 16% of adult females ($n = 19$) (64). The statistically significant sex-based difference in auditory exostoses (Fisher's exact; $P = 0.002$; $n = 26$) hints at sex-based division of labor (and perhaps leisure) as related to swimming and diving in the cold Pacific waters, although this activity certainly was not exclusive to men. Thus, these combined data are revealing economic/occupational specializations between and within communities; for the latter, it reveals an experiential aspect of life that was likely shaped by sex/gender.

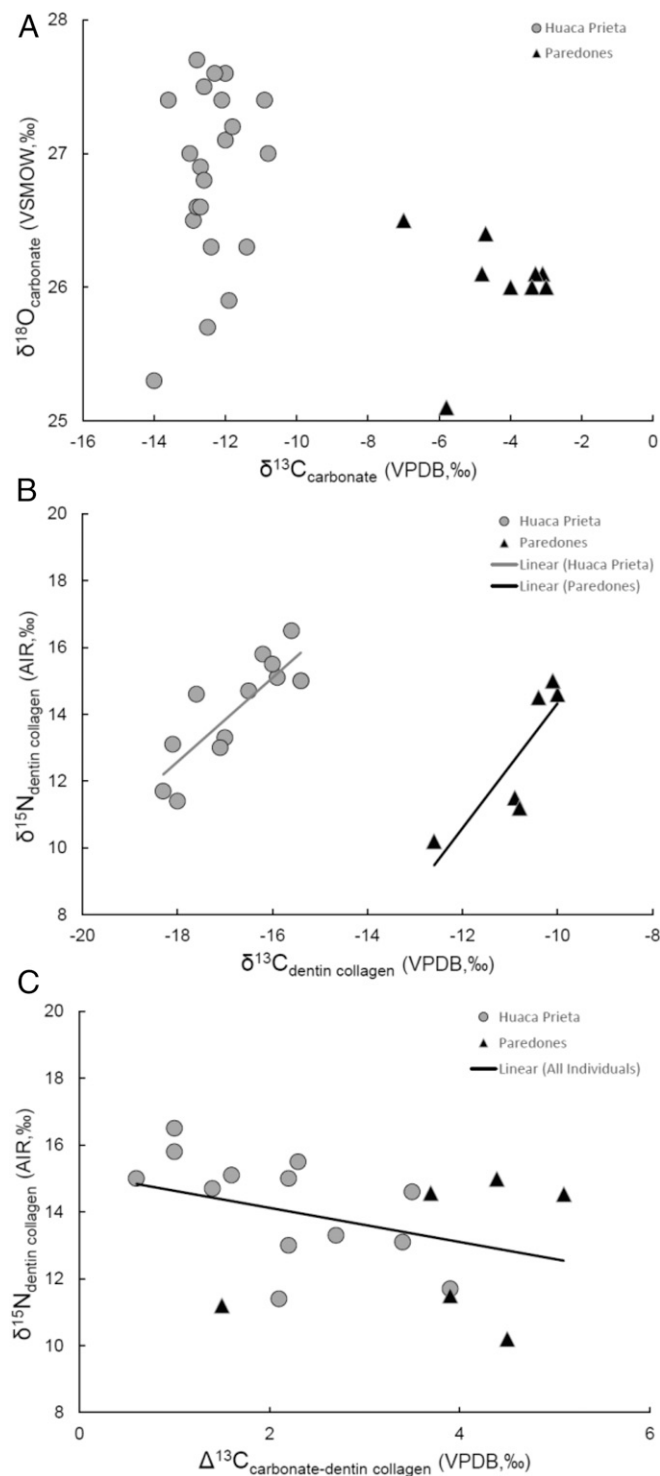


Fig. 2. Stable isotope data of all individuals sampled from Huaca Prieta and Paredones in coastal Peru. (A) Biplot of $\delta^{13}\text{C}_{\text{carbonate}}$ and $\delta^{18}\text{O}_{\text{carbonate}}$ values from Huaca Prieta (circles) and Paredones (triangles), with Paredones individuals having significantly higher $\delta^{13}\text{C}_{\text{carbonate}}$ values and lower $\delta^{18}\text{O}_{\text{carbonate}}$ values than Huaca Prieta individuals. (B) Stable carbon and nitrogen isotope values from dentin collagen from Huaca Prieta and Paredones, each demonstrating a significant relationship between carbon and nitrogen values (respectively: $P = 0.0003$, $R^2 = 0.71$; $P = 0.033$, $R^2 = 0.72$). (C) Relationship between $\Delta^{13}\text{C}_{\text{carbonate-dentin collagen}}$ and $\delta^{15}\text{N}_{\text{dentin collagen}}$ ($P = 0.117$, $R^2 = 0.14$, for individuals from both sites). Note that all $\delta^{13}\text{C}_{\text{carbonate}}$ values were adjusted by 2.3‰ prior to calculating $\Delta^{13}\text{C}_{\text{carbonate-dentin collagen}}$ (47).

Additional clarification on diets was explored by applying three analytical models with the adjusted and unadjusted $\delta^{13}\text{C}_{\text{enamel carbonate}}$ values (*SI Appendix*), and all three starkly reveal the distinct diets between the two sites. The $\Delta^{13}\text{C}_{\text{enamel carbonate-dentin collagen}}$ values show that at Huaca Prieta there is a heavy reliance on marine resources and C_3 plants (e.g., non-maize) (Fig. 2 and *SI Appendix*, Fig. S3). However, the $\Delta^{13}\text{C}_{\text{enamel carbonate-dentin collagen}}$ range suggests that Huaca Prieta children were not eating identical diets, as some had more access to terrestrial meat or other ^{13}C -depleted foods (i.e., those individuals with the greater $\Delta^{13}\text{C}_{\text{enamel carbonate-dentin collagen}}$). The Paredones children, in contrast, show greater consumption of terrestrial meat and half of the Paredones individuals sampled consumed more C_4 carbohydrates (e.g., maize) than their site peers and substantially more than children at Huaca Prieta. Although there is clear dietary specialization between the two mound groups, the minor variations within sites suggest possible exchange between communities, revealing nuances of this Pre-ceramic political economy (discussed below and in *Conclusions: Effects of Dietary Practices on Economies and Lifestyles*).

The model by Kellner and Schoeninger (49), with both adjusted and unadjusted $\delta^{13}\text{C}_{\text{enamel carbonate}}$ values, shows distinct clusters, again highlighting the dietary specializations of each community (*SI Appendix*, Fig. S4). This model clearly reveals the dietary significance of nonmaize plants and other ^{13}C -depleted carbohydrates and lipids at Huaca Prieta, while at Paredones, there is a predominant role of C_4 energy sources (e.g., maize). Given that we ran the model with both unadjusted and adjusted values, we highlight the general similarities between both, but the version with adjusted $\delta^{13}\text{C}_{\text{enamel carbonate}}$ values shows that some Paredones children had minor dietary contributions from C_3 energy sources such as nonmaize plants. The model by Froehle et al. (50) also shows that the Huaca Prieta individuals cluster separately from the Paredones individuals, further substantiating the key point that these neighboring groups had major dietary differences (discussed below and in *Conclusions: Effects of Dietary Practices on Economies and Lifestyles*). Many of the sampled Huaca Prieta children are trending toward Cluster 3, suggesting marine foods as a protein source, which accords with the higher $\delta^{15}\text{N}$ values at Huaca Prieta (Fig. 2). However, there are a few at Huaca Prieta who consumed substantial quantities of terrestrial meat during childhood (Cluster 1). This variability in childhood diets indicates access to foods that their specialized marine-based community may not have produced themselves. This suggests exchange with other groups that did not specialize in marine-resource extraction but perhaps focused on terrestrial food resources. Interpreting these data on a broader theoretical plane also reveals structural factors related to differential access to resources, perhaps shaped by political decision-making, kinship affiliations, and cultural notions regarding which foods and drink are appropriate to consume (65, 66). Moreover, the agential capacities of children and family members can also influence what a person consumes, showing how dietary variability in a community can also be influenced by personal preferences.

In contrast to Huaca Prieta childhood diets, all three models (with both corrected and uncorrected $\delta^{13}\text{C}_{\text{enamel carbonate}}$ values) show that Paredones children consumed significant quantities of maize and a mix of terrestrial C_3 and C_4 proteins; the latter could include marine foods, terrestrial animals that consumed C_4 plants, top predator lake fish (67, 68), and/or protein-rich amaranth (Figs. 2 and 3, Table 1, and *SI Appendix*, Figs. S3 and S4 and Table S1). The predominance of maize in children's diets at Paredones is clear in the model by Froehle et al. (50), where all are in and near Cluster 2, showing that $\sim 70\%$ of their diet was from C_4 plants (Fig. 3). While there are other C_4 plants in the Andes (e.g., amaranth) that exhibit $\delta^{13}\text{C}$ values similar to maize (69, 70), botanical data (33, 71) support the interpretation that maize was the primary C_4 plant food eaten at Paredones (33, 71).

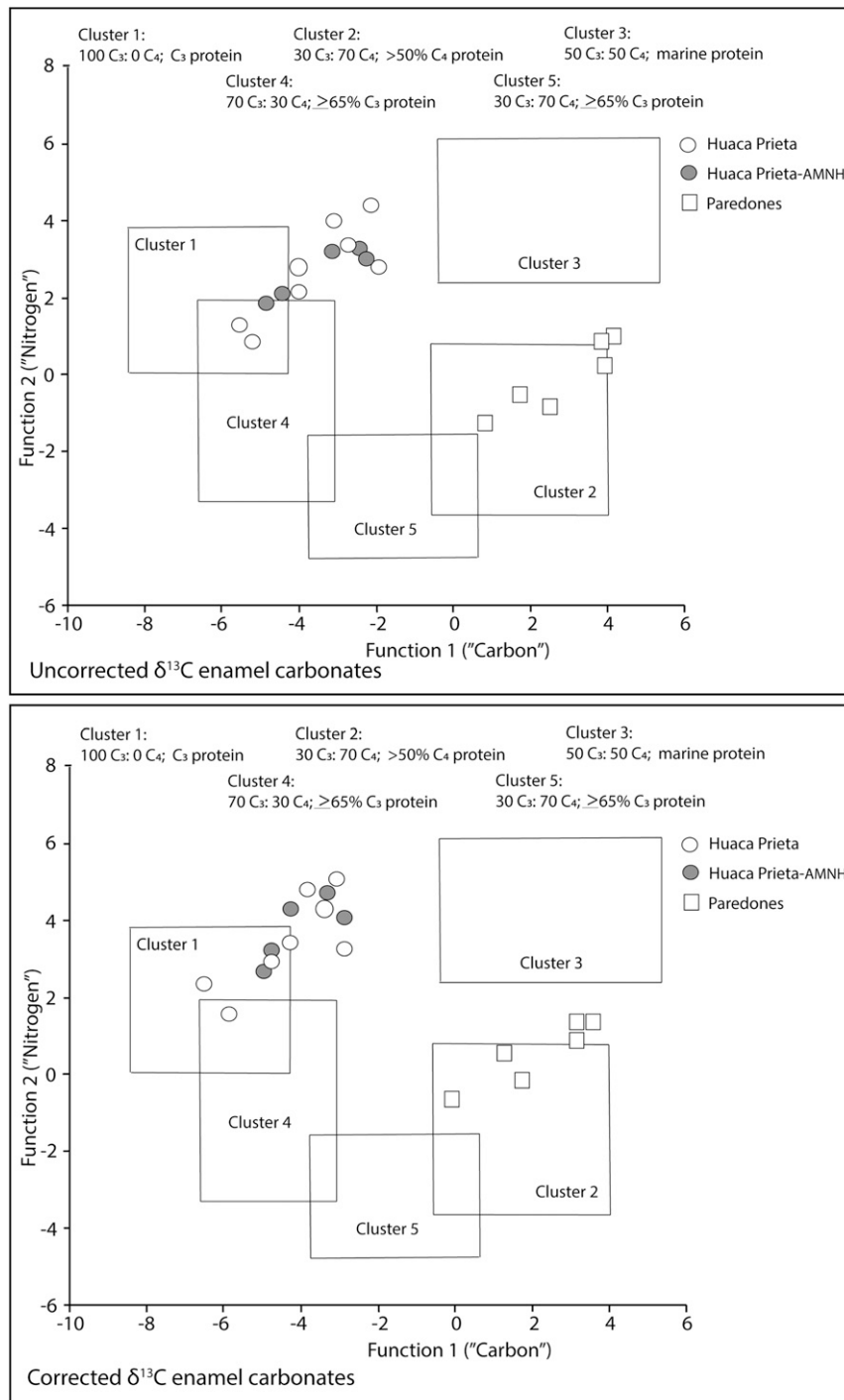


Fig. 3. Application of the model by Froehle et al. (50) to stable carbon and nitrogen isotope data from Huaca Prieta and Paredones individuals, run with uncorrected (A) and corrected (B) $\delta^{13}\text{C}_{\text{enamel carbonate}}$ values. (A) Uncorrected $\delta^{13}\text{C}$ values from enamel carbonates. (B) Corrected values (-2.3‰) applied to $\delta^{13}\text{C}$ values from enamel carbonates to account for the enrichment of ^{13}C in enamel apatite relative to bone apatite (23). Paredones individuals fall within and on the edges of Cluster 2, defined as consuming greater than 50% C_4 protein and 70% C_4 foods (e.g., maize). About half of the Huaca Prieta individuals fall within Cluster 1, indicative of a high proportion of C_3 carbohydrates and C_3 protein, while the others are outside of Cluster 1, trending toward Cluster 3, suggesting a mix of marine and terrestrial protein sources.

Given that maize is a staple food in childhood diets at Paredones, it may have been consumed as a weaning food in the form of corn gruel and/or *chicha* (maize beverage, fermented or unfermented). Popcorn, although it appears early in the Pre-ceramic sequence at Huaca Prieta, would not have been a good weaning food because it can be a choking hazard, and young

children have few deciduous teeth for chewing. Corn gruel and *chicha*, on the other hand, with their soft texture and liquid form, respectively, are ideal dietary items for weaning. Given the high $\delta^{13}\text{C}$ values for Paredones childhood diets, it is likely that maize gruel was more commonly used as a weaning food than *chicha*, the latter of which has a lower maize to water ratio than maize

gruel. It is also possible that breastfeeding women consumed maize, thus passing on the elevated $\delta^{13}\text{C}$ values to the breastfed infants. Although we do not have $\delta^{13}\text{C}$ data from adult bones to reconstruct adult diet, the dental microwear data suggest that maize prepared on a grinding stone was consumed. Thus, the cultural pathway through which maize became a staple food may not have been associated solely with adult dietary demands; the needs of infants and breastfeeding mothers would have been a powerful impetus for producing maize.

Maize cobs and husks were recovered at both the Huaca Prieta and Paredones mounds, albeit primarily the latter (33). At Huaca Prieta, early maize production was documented between 6,734 and 6,569 cal B.P. based on the presence of dated husks and shanks, and maize in the form of popcorn dates to ~6,500 cal B.P., followed by *chicha*, and later corn meal in subsequent millennia (32, 33). Earlier studies showed no clear evidence that maize was a staple food in the area before ~5,000 to 4,500 cal B.P. due to the discontinuous nature of macro- and microfossils (33) and the rarity of grinding stones for processing maize. However, this study provides direct evidence of significant maize consumption by Paredones individuals by at least 6,500 to 6,000 cal B.P. This is a significant finding, showing that maize may have been a staple crop earlier than previously thought (33). Moreover, although economic specialization has been documented among different segments of late Pre-ceramic littoral population at Bandurria on Peru's central coast (72) and for later ceramic cultural periods (after ~4,000 cal B.P.) (15), this study demonstrates maritime and terrestrial economic specialization along the north Peruvian littoral by at least 6,500 to 6,000 cal B.P.

Dental microwear attribute values (i.e., significantly higher complexity values on Paredones teeth relative to Huaca Prieta) are consistent with a diet of increased abrasives associated with maize consumption, likely due to the processing of maize on grinding stones (52). Further, the noted differences in DMTA attribute values between prehistoric populations correspond with known differences in diet and food-preparation techniques, with the Fuegians and Chumash primarily consuming marine meat with low abrasives, the Khoe-San being intermediate hunter-gatherers, and the Andamanese and Tigara preparing/storing their food in ways that allowed for the ingestion of significant abrasives (46). The dietary differences observed between the neighboring communities of Huaca Prieta and Paredones is likely tied to the economic specializations that each created and maintained as part of other highly localized cultural traditions that included distinct food production strategies, weaving techniques, and symbols on decorated gourds and other artifacts (73).

Water Sources, Preparation, and Migration. To compare the $\delta^{18}\text{O}$ values between water samples and the human enamel carbonates, the latter were converted to $\delta^{18}\text{O}_{\text{dw-VSMOW}}$ (*Materials and Methods*), and results show that the Huaca Prieta mean $\delta^{18}\text{O}_{\text{dw-VSMOW}}$ is -6.3 ± 0.9 and the Paredones mean is -7.4 ± 0.5 and that the human enamel carbonates are significantly more enriched than the local water obtained by our study and previously published values from the nearby Moche River and canals (74) (Mann-Whitney *U* test; $P = 0.009$) (Fig. 4). However, the difference falls within the MMD outlined by Pestle et al. (51). Furthermore, the systematic offset between the $\delta^{18}\text{O}_{\text{dw-VSMOW}}$ values from water samples and the converted enamel carbonates could be explained by imperfect formulas for converting the $\delta^{18}\text{O}$ values in enamel carbonates to make them comparable to drinking water. This is because studies are still needed to understand the fractionation effects when routing oxygen isotopes to various mammalian tissues (75–78). Notably, the $\delta^{18}\text{O}$ values from enamel carbonates are systematically more enriched than the water, rather than showing values that are variable (both depleted and enriched). The latter would have suggested that individuals were obtaining water from a wider variety of sources,

some of them even nonlocal. Another possibility is that the enriched $\delta^{18}\text{O}$ values in humans may suggest that communities were boiling and/or fermenting beverages. As water is boiled and sits during fermentation, the lighter ^{16}O evaporates, resulting in enriched $\delta^{18}\text{O}$ values (74, 79). These considerations help to clarify why the $\delta^{18}\text{O}$ values from enamel carbonates are enriched relative to water in the region, further demonstrating that these individuals did not spend their childhoods in distant locales or higher altitudes. The oxygen isotope data suggest that the Huaca Prieta and Paredones individuals are from the northern, coastal regions of Peru.

Furthermore, the homogenous $\delta^{18}\text{O}_{\text{enamel carbonate}}$ values suggest that nonlocal individuals are not present at either site. This is demonstrated by the raw (unconverted) oxygen isotope data from the humans, which show low SDs within each site of $<1\text{‰}$ (0.5‰ at Paredones and 0.9‰ at Huaca Prieta). These data are consistent with the interpretation that these two mounds may have been reserved for local community members, at least in the early centuries of their use. Thus, the differences in dietary isotope data presented in *Results* are likely not a function of nonlocal people (with distinct diets from far-away lands) moving to the area after childhood or being brought to Huaca Prieta or Paredones for burial. Future strontium- and lead-isotope studies could further support or refute this interpretation.

Conclusions: Effects of Dietary Practices on Economies and Lifestyles.

In summary, four major conclusions can be drawn. First, although previous studies had postulated that maize did not become a regular food crop until ~5,000 to 4,500 cal B.P., an interpretation primarily based on low quantities of maize and grinding stones at Paredones and Huaca Prieta (33, 34), we now suggest that maize had an important dietary role by at least 6,500 to 6,000 cal B.P. at Paredones. This is based on the isotopic and dental microwear evidence presented here and supported by previous work on micro- and macrobotanics and grinding stones (32, 38). It is possible that the Paredones population was an isolated enclave along this area of the coast that adopted and incorporated maize early into the diet. This early maize adoption may not be the case at contemporaneous and later sites in the Central Andes, where maize appears more regularly in the archaeological record ~5,000 to 4,500 cal B.P. (19, 39, 80). Second, the stable isotope data show that the two communities had highly distinct childhood diets; Huaca Prieta focused on marine foods and C_3 plants, while Paredones children primarily consumed maize and terrestrial meat with some marine and/or terrestrial meat that was ^{13}C -enriched. The maize consumed by infants and young children was likely in the form of gruel and/or *chicha*, owing to their suitable properties as weaning foods. Third, those dietary specializations persist into adulthood, as substantiated by dental microwear data from both sites and the high frequency of auditory exostoses among Huaca Prieta adults. Fourth, oxygen isotope values are tightly clustered in all sampled data, suggesting that the individuals from both sites are local. There is no current

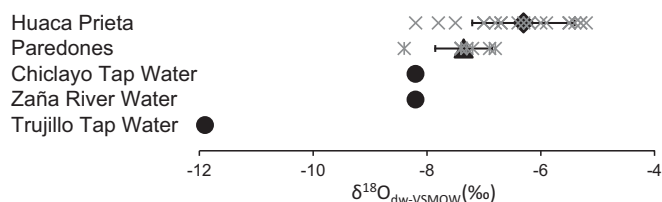


Fig. 4. Stable oxygen isotopes from individuals at Huaca Prieta and Paredones, as compared to local-modern water sources. $\delta^{18}\text{O}_{\text{dw-VSMOW}}$ values from Huaca Prieta (gray X symbols and black diamond) and Paredones (gray * symbols and black triangle) with 1 SD ($n - 1$) noted. Local-modern water sources are noted (black circles).

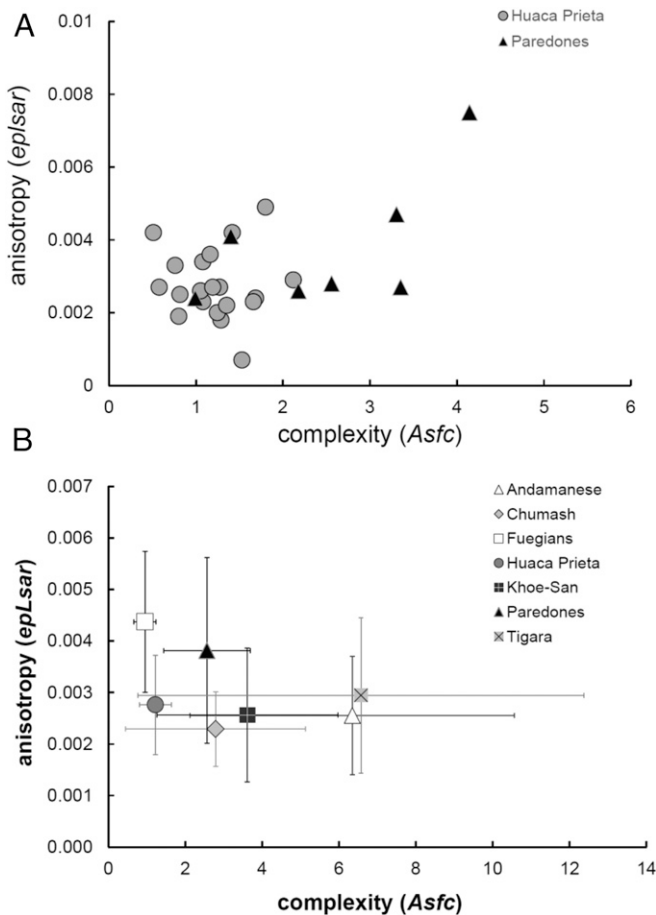


Fig. 5. DMTA attribute values of individuals sampled from Huaca Prieta and Paredones mounds in coastal Peru. (A) Complexity (Asfc) and anisotropy (epLsar) values of Huaca Prieta and Paredones individuals. (B) DMTA attribute values as compared to prehistoric populations (46). Huaca Prieta individuals are most similar to Fuegians (Tierra del Fuego, marine-based economy) and have significantly lower complexity values than Paredones individuals. Paredones individuals have significantly higher complexity than Huaca Prieta individuals ($P = 0.037$), indicative of higher abrasives in their diet and coincident with higher maize inputs.

evidence to suggest individuals are from distant zones. This finding is important because it suggests that dietary differences are not a function of people from different geographic areas.

In building on prior research (28), these findings show that a mosaic of tightly juxtaposed ecological niches and other factors along the Chicama littoral promoted local economic specialization by household communities associated with Huaca Prieta and Paredones at least by ~6,500 cal B.P. This specialization intensified between 6,500 and 4,000 y ago and promoted an exchange economy between and beyond local littoral and nearby terrestrial communities and ultimately stimulating increases in social and economic diversity and complexity.

A major advantage of prolonged economic specialization for these local communities would have been lower procurement cost of resources and higher production efficiency. That is, specialized farmers, fisherfolk, and shellfish gatherers were likely more skilled at growing and gathering certain resources because they would have been more familiar with their seasonal availability and habitat patterns. Specialization also can imply greater social solidarity within and between communities by working and living together in the same setting and by focusing on specific products and the innovative technologies (e.g., cotton fishing

nets, fishhooks, lithic blades) required to process them. There are wider sociopolitical implications as well. For instance, a dual economy is a specialized organizational structure, which likely would have distinguished leadership, roles, and responsibilities for the different population segments. This would have allowed the breakdown of individual tasks into smaller more precise steps (e.g., food procurement, preparation, distribution), which, in turn, would have created more levels of vertical and horizontal complexity and more opportunities for community growth, cooperation, and leadership. Although there is complexity in the form of the monumental architecture at Huaca Prieta, the symbols on gourds, textiles, and other items at various sites (73) and, to a certain degree, specialization itself, there is no clear material evidence for intergroup competition and centralization of power and authority. The absence of elaborate houses and tombs at Paredones, Huaca Prieta, and outlying residential sites suggests no formal or permanent leadership and social stratification, although there is some social differentiation, as indicated by numerous distinct weaving techniques and by community identity markers, such as symbols on carved gourds and cotton textiles (73). Given these artifact differences, the dietary differences identified from isotope and dental microwear texture data further clarify the distinct, yet complementary ways that these neighboring communities organized resource production and exchange.

There are possible downsides to specialization (overspecialization) that can contribute to dependence on others for vital resources and food shortages, especially during times of social unrest or major environmental stress such as droughts, El Niño, and tsunami floods (81, 82). Although specialization potentially would have erected some barriers between different specialized groups, which could have led to communication and exchange problems, there is no evidence of this. Rather, cooperation and nonviolence are suggested by the absence of both weaponry and skeletal trauma (41) and by a public place—especially the Huaca Prieta mound—shared by the two communities. Given the evidence for possible marine protein consumption among a few individuals at Paredones, it appears that the Paredones community either obtained marine resources on their own or exchanged terrestrial and agricultural items with littoral, fishing communities, such as the local communities engaged in ritual at Huaca Prieta. The presence of maize husks and cobs at Huaca Prieta (32) suggests that there was a reciprocal flow of goods, even though there is little to no isotopic evidence of maize consumption among Huaca Prieta children and no dental microwear data suggesting that adults ate maize processed on grinding stones. In synthesizing these various lines of data, it is possible that Huaca Prieta adults consumed maize only occasionally, perhaps in feasting and mortuary rituals and regionally communal settings that included the exchange and consumption of certain food items.

The data presented here, in combination with previously published data on fauna (31), botanics (32, 33), grinding stones, and other artifacts (34), suggest that subsistence specialization, combined with limited exchange of food items, was a key organizing force for these early, littoral groups. The notion that each community was procuring and producing a variety of dietary resources—as would be expected by the vertical archipelago model (24)—is not supported by these data. Instead, each community developed specialized knowledge and skills that supported the focused exploitation and production of particular dietary resources that they occasionally exchanged, an economic strategy that can have far-reaching effects. Indeed, the exchange of food items tied these communities together, creating sociopolitical connections that are also evident in the architectural and spatial layout at Huaca Prieta, where small groups from the two communities gathered in discrete ritual spaces to create and sustain those ties of reciprocity. Broadly, these data reveal the temporal depth of occupational specializations in littoral groups, a form of resource-procurement organization that was also

practiced by late pre-Hispanic groups in littoral and interior coastal areas (15, 21). The extent to which this form of occupational specialization was continuous through time or shifted depending on ecological conditions, regional politics, and other variables remains an open question, but it is clear that it has origins in the middle Preceramic era on the north coast of Peru. In later times, however, it appears that some societies were less specialized, although they gave primary emphasis to either marine or crop foods. For instance, at the Gramalote site (3,500 to 1,350 cal B.P.), inhabitants practiced mixed fishing and farming and exchanged marine and other littoral foods for crops from interior valley farmers (19). The subsistence patterns of these and other later, hierarchically based communities were influenced more by political and social factors than earlier egalitarian groups such as those in the Huaca Prieta area. Regardless of temporal affiliation, studies of food consumption require combined data from isotopes, dental microwear, flora, fauna, and associated extractive and production tools. A sole focus on food debris primarily yields insights on specialized food production and exchange, rather than the actual local dietary patterns.

Our knowledge of early socioeconomic exploration, innovation, and development, and the antecedents and consequences of these activities, remains unclear in the study of early civilizations. We specifically advance here some mechanisms by specialized, coexisting groups to establish an integrative, noncentralized, complementary community organization. Not studied here due to the lack of evidence are intra- and interconnectedness within and between these communities, which appear to be important antecedents of exploratory social and economic innovation. Also not examined is the effect of dynamic, closely juxtaposed microenvironments in the study area that either facilitated or stimulated economic specialization. Nonetheless, we hope this study contributes greater clarity and insights on the foundations and influences upon which later societies in the Andes and elsewhere developed urbanism and more complex sociopolitical structures.

Materials and Methods

The human skeletal remains in this study were excavated in different mortuary and discard contexts at Huaca Prieta and Paredones, respectively; the samples from both sites date to ~6,500 to 4,000 cal B.P. (38). Dental samples from 21 Huaca Prieta individuals and 9 Paredones individuals were examined (*SI Appendix, Table S1*). (See *SI Appendix* for information on archaeological context of the human samples.)

Stable Isotope Analyses. All of the Huaca Prieta and Paredones dental samples were analyzed for stable carbon and oxygen isotopes from enamel carbonates, and stable carbon and nitrogen isotopes were analyzed from the tooth dentin collagen from 13 individuals at Huaca Prieta and 6 individuals from Paredones and from 2 faunal bones from Paredones (Table 1 and *SI*

Appendix, Table S1). Surface-water samples were analyzed for stable hydrogen and oxygen isotope ratios (*SI Appendix*).

To elucidate protein and carbohydrate sources among the two populations, we examine the stable isotopes from different tissues using three distinct models: 1) the $\Delta^{13}\text{C}_{\text{enamel carbonate-dentin collagen}}$ values (42, 44); 2) the Kellner and Schoeninger model (49) that compares $\delta^{13}\text{C}_{\text{carbonates}}$ and $\delta^{13}\text{C}_{\text{collagen}}$ to results from animal-feeding studies and populations with well-studied diets; and 3) the model developed by Froehle et al. (50), which assesses the $\delta^{13}\text{C}_{\text{coll}}$, $\delta^{13}\text{C}_{\text{carb}}$, and $\delta^{15}\text{N}_{\text{coll}}$ values together to better discern protein sources (*SI Appendix*). All three models were originally developed with bone carbonate and bone collagen, and while other scholars have done apatite-collagen spacing analysis with enamel apatite and dentin collagen (83), here, we incorporate a correction of 2.3‰ for $\delta^{13}\text{C}$ values from enamel apatite to account for its ^{13}C enrichment relative to bone apatite (84) (*SI Appendix*).

DMTA. Molars from all individuals exhibiting wear were molded and subsequently cast for DMTA. DMTA was performed on crushing/grinding facets (e.g., facet 9) of all tooth casts that preserved antemortem microwear using white-light confocal profilometry and scale-sensitive fractal analysis (similar to refs. 85, 86) (*SI Appendix*).

Statistical Analyses. All statistical analyses followed the same methods of a prior geochemical and DMTA analysis. Statistical comparisons of stable isotope data employed Student's *t* tests; however, when there was a significant difference in the variance of the samples, a Mann-Whitney test was performed. In the case of the $\delta^{18}\text{O}_{\text{enamel carbonate}}$ values, a Mann-Whitney test was used, as these data were nonnormally distributed ($P = 0.023$ for Paredones individuals; Shapiro-Wilk tests). All DMTA attributes were statistically compared to the raw data from El-Zaatari (46), allowing individuals from Huaca Prieta and Paredones to be compared to five historic/prehistoric hunter-gatherer populations with diverse dietary behaviors (*SI Appendix*). Statistical comparisons used Kruskal-Wallis tests and multiple comparisons using Dunn's procedure, as DMTA data are nonnormally distributed (as indicated via Shapiro-Wilk tests). Mann-Whitney *U* tests were also used to compare DMTA attributes between Huaca Prieta and Paredones populations.

Data Availability. All study data can be found in the text and *SI Appendix*.

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