Quinoa, potatoes, and llamas fueled emergent social complexity in the Lake Titicaca Basin of the Andes

Melanie J. Miller[a,b,1], Iain Kendall[c], José M. Capriles[d], Maria C. Bruno[e], Richard P. Evershed[c], and Christine A. Hastorf[b,f,1]

[a]Department of Anatomy, University of Otago, Dunedin 9054, New Zealand; [b]Archaeological Research Facility, University of California, Berkeley, CA 94720; [c]Organic Geochemistry Unit, School of Chemistry, University of Bristol, Bristol BS8 1TS, United Kingdom; [d]Department of Anthropology, The Pennsylvania State University, University Park, PA 16802; [e]Department of Anthropology and Archaeology, Dickinson College, Carlisle, PA 17013; and [f]Department of Anthropology, University of California, Berkeley, CA 94720

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The Lake Titicaca basin was one of the major centers for cultural development in the ancient world. This lacustrine environment is unique in the high, dry Andean *altiplano*, and its aquatic and terrestrial resources are thought to have contributed to the florescence of complex societies in this region. Nevertheless, it remains unclear to what extent local aquatic resources, particularly fish, and the introduced crop, maize, which can be grown in regions along the lakeshores, contributed to facilitating sustained food production and population growth, which underpinned increasing social political complexity starting in the Formative Period (1400 BCE to 500 CE) and culminating with the Tiwanaku state (500 to 1100 CE). Here, we present direct dietary evidence from stable isotope analysis of human skeletal remains spanning over two millennia, together with faunal and floral reference materials, to reconstruct foodways and ecological interactions in southern Lake Titicaca over time. Bulk stable isotope analysis, coupled with compound-specific amino acid stable isotope analysis, allows better discrimination between resources consumed across aquatic and terrestrial environments. Together, this evidence demonstrates that human diets predominantly relied on C_3 plants, particularly quinoa and tubers, along with terrestrial animals, notably domestic camelids. Surprisingly, fish were not a significant source of animal protein, but a slight increase in C_4 plant consumption verifies the increasing importance of maize in the Middle Horizon. These results underscore the primary role of local terrestrial food resources in securing a nutritious diet that allowed for sustained population growth, even in the face of documented climate and political change across these periods.

dietary reconstruction | stable isotopes | amino acids | agropastoralism | subsistence resilience

Food systems play an integral role in human societies, and reconstructing subsistence practices is a key component for understanding human evolution and cultural change (1–3). A hallmark anthropological categorization of societies centers on subsistence labels such as “hunter-gatherers,” “agriculturalists,” “fisherfolk,” etc., and the study of changes or combinations among these strategies of resource use has been central to archaeological research. Foodways can be particularly informative about cultural vulnerabilities or resilience in a society’s response to intrinsic and extrinsic forces, such as population increase or climate change (4–6). Food security, including sufficient and stable access to nutritious resources, is fundamental for supporting demographic growth and increasingly complex social systems. Archaeological studies of ancient food practices have shed light on how human groups have utilized various resources and harnessed knowledge to transform the world around them through a diversity of food foraging and producing strategies, especially during times of political change (7–9). Shifts in foodways are given as both a motivation for and as evidence of critical societal transitions, including changes in social complexity (8, 10, 11).

In this work, we approach social complexity from a diachronic perspective in relation to sociopolitical scalar power. In the Lake Titicaca Basin of the Andes, we see dynamic changes in political structures over time as smaller dispersed communities developed ceremonial centers and expanded networks of social-political-economic relations that, over centuries, entangled formerly disparate groups into larger polities. Shared practices of material culture in pottery, textiles, architecture, and even food culminated and were transformed into a centralized sociopolitical entity at the site of Tiwanaku, which most scholars regard as a state (12–14). By exploring human food procurement through the lens of stable isotope signatures from bulk and compound-specific amino acid (CSAA) fractions from human, plant, and animal remains recovered from archaeological sites, we probe how changes and continuity in food consumption drove and enabled cultural continuity and change in the southern Lake Titicaca basin prior to and during the development of the Tiwanaku state.

Straddling modern-day Bolivia and Peru at 3,810 m above sea level and extending over 8,300 km^2, Lake Titicaca creates a unique environment in the cold, dry Andean *altiplano* (Fig. 1). The lake supports rich aquatic resources, such as birds, fish, and plants, notably the *totora* reed, and productive terrestrial

Significance

Food production systems are critical components in the emergence of complex socioecological systems. In the Andes, societal complexity has often been related to the increasing production and consumption of maize by elites, but the importance of highland cultivated crops, such as potatoes, one of the most cultivated crops in the world, and quinoa, presently recognized as a “superfood,” remains largely underappreciated. Using stable isotopes including compound-specific amino acids, we reconstruct the diets of people living in southern Lake Titicaca, where the Tiwanaku state emerged. Over time, locally produced potatoes, quinoa, and llamas, by means of increasingly intensive practices, facilitated long-term food security, which sustained population growth, contributed to increasing sociopolitical complexity, and facilitated resiliency through episodes of significant climatic variation.

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[1] To whom correspondence may be addressed. Email: melanie.miller@otago.ac.nz or hastorf@berkeley.edu.

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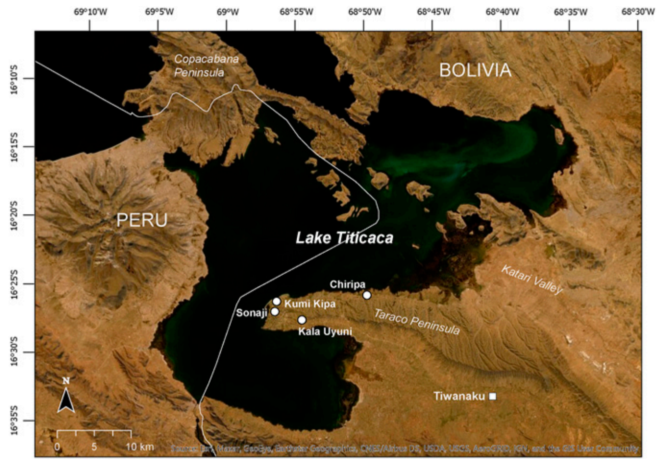

Fig. 1. Map of the Taraco Peninsula and the southern Lake Titicaca basin, Bolivia. The circles indicate excavated sites discussed in text, and the square indicates the center of the Tiwanaku state.

resources, due to relatively greater rainfall and warmer temperatures than the surrounding highland regions (15, 16). Today, this environment supports highly productive agropastoral and fishing communities, yet many questions remain about the evolution of this unique socioecological system over the past three millennia. At the time of Spanish conquest in 1532 CE, the shores of Lake Titicaca sustained some of the densest human populations in the Andes (12, 13). Long-term archaeological research in the region verifies that food producing societies emerged in the basin around 1400 BCE, and successive generations of community growth, fission, and integration followed from 500 to 1100 CE, coalescing into a macroregional primary state known as Tiwanaku (17–20). Throughout this sequence, agriculture played a critical role as suggested by archaeological remains of crops such as quinoa and tubers, as well as sustained investment in infrastructure intensification, such as decreasing fallows, construction of hundreds of hectares of raised fields, irrigation canals, and water reservoirs (14, 21, 22). Evidence for large-scale camelid pastoralism is present in the zooarchaeological record as well as later historical accounts of large Inca herds (23–25). The ready resource of lake fish was also believed to provide another critical protein source to local populations (16, 26).

The surface of Lake Titicaca has fluctuated considerably at decadal and centennial scales over the course of the Holocene due to changes in rainfall and evapotranspiration (27, 28). While paleoecological evidence suggests that these terrestrial and aquatic food sources persisted over time with these environmental changes (27), the relative contributions of each to human diets remains uncertain. Finally, as people, products, and ideas circulated via increasingly broader exchange networks beyond the basin, it is still unclear how exotic foods, such as maize, catalyzed regional processes of political integration in the Formative times before Tiwanaku grew.

Maize has a unique history as a plant that was incorporated into numerous South American cultures and cuisines at different times and to different degrees and has had various meanings and roles ascribed to it (29–32). Maize, particularly in the form of alcoholic chicha beer, has been linked to cultural complexity through its use in state economics and politics, including sponsored redistributive feasts, such as in the Tiwanaku, Wari, Chimu, and Inka states (31, 32), but this may also obscure the roles of other foods in catalyzing changes that were necessary agents/precursors for the development of those states. The focus on the political role of maize in Middle Horizon polities, including Tiwanaku, may have caused archaeologists to overlook other key foods that underpinned the ability for those communities to have been sustained for so long. Within the Tiwanaku context, the use of maize at the political center of Tiwanaku is well documented as a symbolically charged food (14, 22, 30, 33). Maize, however, cannot grow well in this extreme *altiplano* environment except along the shores of Lake Titicaca, making this the only place where a specific, small cob variety of maize can be grown. We are still seeking clear data for when this variety was successfully adapted to shoreline production systems, but there are hints that maize in the Formative times that could have been traded in or else grown locally and clear evidence for regional leaders organizing the production and importation of maize in lower elevation communities (30, 34, 35). The evidence for maize beer use in redistributive feasts is well documented at Tiwanaku, as a portion of the population regularly consumed maize (33). However, the history of successful maize selection in the Titicaca basin requires more research to clarify this timing, and dietary studies could contribute to this debate.

While the lake provided a unique *altiplano* environment for agriculture, pastoralism, collecting aquatic resources including fish, and facilitating movement and trade, how human communities utilized the lake to manage food security, variability, and stability over time remains largely undefined. Stable isotopic analysis is one of the only ways to directly reconstruct dietary practices of individuals in the past and can provide key insights into the importance of different foods within a community and across time, particularly how specific foods contributed to population growth and increasing social complexity.

Archaeological Evidence of Subsistence on the Taraco Peninsula

Long-term archaeological research on the Taraco Peninsula, situated between Lake Wiñaymarka, the southern portion of Lake Titicaca, and the northern boundary of the Tiwanaku valley, has provided detailed datasets for reconstructing dynamic subsistence practices including farming, herding, fishing, and foraging over time (18, 21, 23, 26). Robust archaeological data from excavations at the sites of Chiripa, Kala Uyuni, Sonaji, and Kumi Kipa verify that between 1400 BCE and 1100 CE, these lacustrine communities utilized a wide range of plant and animal resources (*SI Appendix*, Supplementary Information Text).

Archaeobotanical evidence indicate that plant foods consisted primarily of domesticated Andean crops (*SI Appendix*, Fig. S1), particularly quinoa (*Chenopodium quinoa* Willd.) and tubers, including potatoes (*Solanum tuberosum* L.) and oca (*Oxalis tuberosa* Molina) (21, 36, 37). Quinoa is ubiquitous across all time periods, with tubers appearing to grow in importance in the Late Formative and Tiwanaku periods (21). The nonlocal domesticated plant food, maize (*Zea mays* L.), is relatively sparse in peninsular contexts until the Tiwanaku period, when it became a central crop of the state (30, 33, 38). Wild plant foods and possibly *totora* reed (*Schoenoplectus californicus* ssp. *tatora*) may have contributed to seasonal meals and snacks (37, 39).

Animal herding was also very important, as documented by the abundant remains of camelids in the archaeological contexts (40). Most bones were intensively fragmented, likely as a consequence of their consumption in stews and soups that maximized the extraction of fat, marrow, and other nutrients (23). Domesticated camelids, but most importantly llamas (*Lama glama* L.), were important not only as food but for their use in transportation and for producing wool and dung, likely used for fuel and fertilizer.

Fish remains are also abundant in all studied sites, and thanks to fine-grained recovery and identification of microfaunal remains, it seems they were ubiquitous over time (26, 41).

Identified fish taxa include various species of the killifish genus *Orestias* as well as a few catfish species of the genus *Trichomycterus*, both of which rarely exceed 20 cm in length. Previous research hypothesized that the use of lake resources may have changed over time in conjunction with shifts in the lake level, such that people may have consumed more aquatic foods when the shore was nearby (42, 43). Recent research, however, has demonstrated that fish bone ubiquity persisted at a high level even during periods of strong lake level variation (26).

Archaeological plant and animal remains ostensibly demonstrate the importance and use of these species by Taraco Peninsular communities, but their relative contributions to diet are difficult to ascertain due to a range of pre- and postdepositional variables. Stable isotopic analysis is one of the only ways to directly reconstruct dietary practices of individuals in the past and provide key insights into the importance of different foods within a community and across time.

Dietary Reconstruction via Stable Isotope Analysis

Stable isotope analysis has made significant contributions to paleodietary studies of ancient human populations from around the world (*SI Appendix*, Supplementary Information Text) (3, 44, 45). Although bulk carbon and nitrogen isotopic values from bone and tooth collagen provide major insights into questions about human subsistence and food choice, we are often left with questions about how particular foods and nutritional components (carbohydrates, proteins, lipids) contributed to skeletal chemistry (46–48). Recent research using CSAA stable isotope analysis has demonstrated the potential to tease apart specific food consumption patterns (49–53). Identifying the different amino acid stable isotope compositions of food groups, such as freshwater and terrestrial animals and plants, allows us to track the contribution of these various resources in individuals' diets. Some amino acids are routed directly from food source to consumer tissue without alteration to their δ^{13}C values and therefore can be used as dietary tracers (49, 54–57). Studies of archaeological remains and the tissues of modern animals raised on controlled diets indicate that the amino acids glycine, phenylalanine, and lysine are especially useful in separating aquatic and terrestrial foods (49, 53). Most significantly, aquatic consumers have $\Delta^{13}C_{\text{Gly-Phe}}$ values above 15‰, while terrestrial consumers' $\Delta^{13}C_{\text{Gly-Phe}}$ values are below 15‰, with many exhibiting values below 12‰ (49, 52, 53, 58–60). Therefore, this $\Delta^{13}C_{\text{Gly-Phe}}$ proxy is extremely valuable for studying dietary patterns in regions with both habitats, especially where C_3 and C_4 plants contribute to human diet together with aquatic resources and have overlapping bulk stable isotope signatures, such as in the Lake Titicaca region. The results presented below show how by combining multiple isotopic proxies (bulk isotope values from collagen and hydroxyapatite, and CSAAs from collagen), hitherto unattainable resolution can be achieved in dietary reconstructions over time in the region.

Results

Plants. Ninety-eight modern terrestrial and aquatic plants, five archaeological carbonized plants, and seven modern animal dung samples were analyzed for bulk carbon and nitrogen stable isotope values [lake plant isotopic data were previously reported in Miller et al. (42)] (Fig. 2*A*, *SI Appendix*, Fig. S2, and Dataset S1). The modern and archaeological terrestrial plant bulk δ^{13}C values follow expected patterning C_3, C_4, and CAM (crassulacean acid metabolism) plants and show a wide range of δ^{15}N values. The bulk δ^{13}C values range from –29.2 to –3.0‰ and δ^{15}N values range from –5.3 to +15.2‰. Within that, the average cultigen bulk δ^{15}N value is +7.6‰, with their values ranging from +0.3‰ (modern beans, Fabaceae) to +12.9‰ (archaeological *Chenopodium* seeds, which likely have a slight positive offset due to carbonization and possible higher value due to fertilizer use) (61, 62). The seven modern animal dung bulk δ^{13}C values range from –26 to –17.1‰, and δ^{15}N values range from +4.4 to +15.4‰, reflecting the isotopic composition of the recent meals those animals (sheep, camelids, guinea pig) consumed.

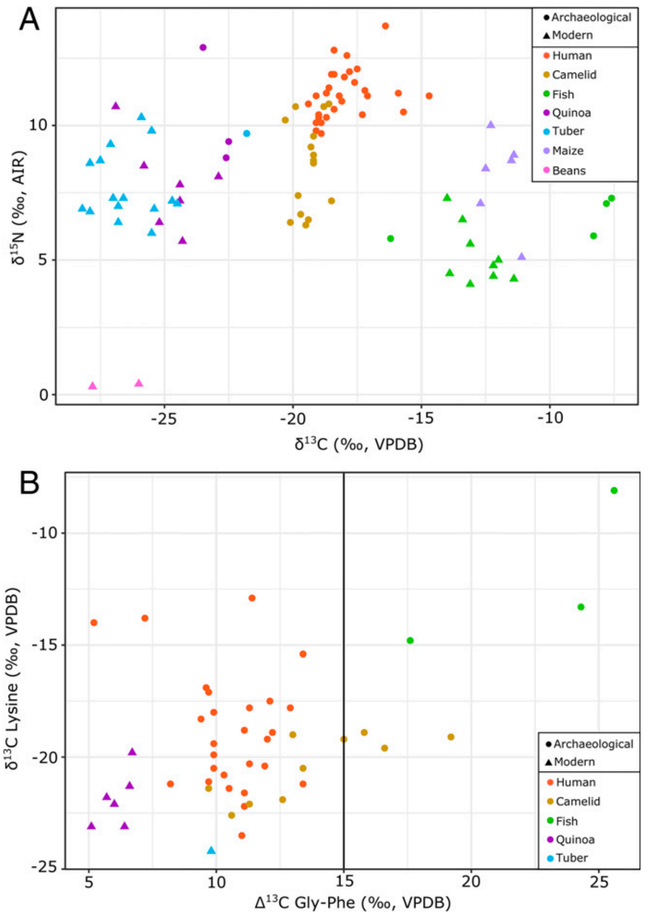

Fig. 2. (*A*) Bulk δ^{13}C and δ^{15}N values for archaeological and modern plants (modern plants δ^{13}C are not Suess corrected), modern and archaeological fish, archaeological camelids, and archaeological humans. (*B*) $\Delta^{13}C_{\text{Gly-Phe}}$ values plotted with $\delta^{13}C_{\text{Lys}}$ for ancient humans, camelids, Lake Titicaca fish, and modern plants. The vertical line at $\Delta^{13}C_{\text{Gly-Phe}}$ = 15‰ follows the findings of Webb et al. (53) and others, indicating the terrestrial versus aquatic protein consumption boundary.

Seven modern plant samples grown on the Taraco Peninsula were analyzed for the $\delta^{13}C_{\text{AA}}$ values of their individual amino acids (Fig. 2*B* and *SI Appendix*, Fig. S3 and Dataset S1). The $\delta^{13}C_{\text{Gly}}$ values range from –20.8 to –16.2‰ (average = –19‰, SD = 1.7‰), $\delta^{13}C_{\text{Phe}}$ values range from –26.9 to –22.9‰ (average = –25.6‰, SD = 1.3‰), $\delta^{13}C_{\text{Lys}}$ values range from –24.2 to –19.8‰ (average = –22.2‰, SD = 1.4‰), and $\Delta^{13}C_{\text{Gly-Phe}}$ values range from 5.1 to 9.8‰ (average = 6.6‰, SD = 1.5‰). The plant amino acid carbon isotope values provide reference points, and of particular importance are the $\Delta^{13}C_{\text{Gly-Phe}}$ values (Fig. 2*B*), which are all below 15‰, as expected for terrestrial species (49, 52, 53, 58–60).

Animals. Sixteen archaeological camelid samples (15 bone; 1 tooth enamel) were submitted to bulk stable isotope analysis (15 for organics, 5 for inorganics; Fig. 2*A*; Dataset S1). The bulk collagen δ^{13}C values range from –20.3 to –18.5‰ (average $\delta^{13}C_{\text{coll}}$ = –19.4‰, SD = 0.5‰). The camelid $\delta^{15}N_{\text{coll}}$ range from +6.3 to +10.8‰ (average $\delta^{15}N_{\text{coll}}$ = +8.5‰, SD = 1.7‰).

The inorganic apatite samples (four bone samples and one tooth enamel sample) have $\delta^{13}C_{ap}$ values ranging from –12.1 to –9.6‰ (average $\delta^{13}C_{ap}$ = –10.8‰, SD = 0.9‰) (*SI Appendix*, Supplementary Information Text). The archaeological camelids' bulk carbon and nitrogen isotope values indicate their diets were dominated by C_3 plants with relatively little input from C_4 or CAM plants (Fig. 2*A*).

Ten archaeological camelid samples were submitted to CSAA (Fig. 2*B* and *SI Appendix*, Fig S3 and Dataset S1), with $\delta^{13}C_{Gly}$ values ranging from –18 to –11.6‰ (average $\delta^{13}C_{Gly}$= –15.4‰, SD = 2.0‰), $\delta^{13}C_{Phe}$ values ranging from –36.7 to –23.9‰ (average $\delta^{13}C_{Phe}$= –29.9‰, SD = 4.1‰), and $\delta^{13}C_{Lys}$ values ranging from –22.6 to –18.9‰ (average $\delta^{13}C_{Lys}$= –20.4‰, SD = 1.5‰). The camelid $\Delta^{13}C_{Gly\text{-}Phe}$ values range from 9.7 to 19.2‰ (average = 13.7‰, SD = 2.9‰). Interestingly, four camelids have $\Delta^{13}C_{Gly\text{-}Phe}$ values above 15‰ (Fig. 2*B*). These results indicate that some camelids primarily consumed terrestrial resources, while others appear to have had diets with significant inputs from near-shore/aquatic plants. The camelid isotope data suggest that there were various herd management strategies or differential land access across individuals, families, or other social grouping, and that local people used markedly different ecological zones in this region to feed their herds (*SI Appendix*, Supplementary Information Text).

Previous isotopic work (42) determined the $\delta^{13}C$ and $\delta^{15}N$ values of modern and ancient fish from Lake Wiñaymarka and a subset of those data are presented here (Fig. 2*A* and Dataset S1). Modern fish bone samples from *Orestias* and *Trichomycterus* genera (n = 9) display bulk $\delta^{13}C$ (lipid-extracted) values ranging from –14 to –11.4‰ and $\delta^{15}N$ (untreated) values ranging from +4.1 to +7.3‰. There are four Taraco Peninsula archaeological fish samples (three bone, one scale) that show $\delta^{13}C$ (lipid-extracted) values ranging from –16.2 to –7.6‰ and $\delta^{15}N$ (untreated) values ranging from +5.8 to +7.3‰ (42). Archaeological *Orestias* sp. fish bone samples (n = 3) were analyzed for amino acid isotope values (Fig. 2*B* and *SI Appendix*, Fig S3 and Dataset S1). Fish $\delta^{13}C_{Gly}$ values range from –3.4 to –1.1‰ (average $\delta^{13}C_{Gly}$= –1.9‰, SD = 1.3‰), $\delta^{13}C_{Phe}$ values range from –27.6 to –18.7‰ (average $\delta^{13}C_{Phe}$= –24.4‰, SD = 4.9‰), and $\delta^{13}C_{Lys}$ values range from –14.8 to –8.1‰ (average $\delta^{13}C_{Lys}$= –12.1‰, SD = 3.5‰). Fish $\Delta^{13}C_{Gly\text{-}Phe}$ values range from 17.6 to 25.6‰ (average = 22.5‰, SD = 4.3‰). The finding that all fish sampled have $\Delta^{13}C_{Gly\text{-}Phe}$ values above 15‰ confirms that this proxy is useful for distinguishing between aquatic and terrestrial habitats in this Andean environment.

Humans. The diets of ancient Taraco peoples are represented by 32 individuals who had a tooth sampled; 31 yielded bulk dentin $\delta^{13}C_{coll}$ and $\delta^{15}N_{coll}$ values, and 28 have bulk enamel $\delta^{13}C_{ap}$ and $\delta^{18}O_{ap}$ values (Figs. 2 *A* and *B* and 3 *A* and *B* and *SI Appendix*, Supplementary Information Text and Figs. S3 and S4 and Dataset S1). Dentin bulk $\delta^{13}C_{coll}$ values range from –19.4 to –14.7‰ (n = 31; average = –18.0‰, SD = 1.1‰), and $\delta^{15}N_{coll}$ values range from +9.7 to +13.7‰ (n = 31; average = +11.1‰, SD = 0.9‰). Given a diet-collagen offset of +5‰ (63, 64), we see that the overall diet averaged –22.9‰, which corresponds to the values of C_3 plants and their consumers. The enamel carbonate $\delta^{13}C_{ap}$ values range from –13.5 to –6.5‰ (n = 28; average = –11.4‰, SD = 1.6‰). Assuming a +12‰ offset between diet and tissue, the average dietary isotopic pool was around –23.3‰, again showing diets were dominated by C_3 plants and their consumers. However, when we examine the humans' bulk carbon isotope values across time periods, we see that many individuals from the Tiwanaku period have slightly higher values, suggesting some consumption of C_4 and/or aquatic foods (Fig. 3*A* and *SI Appendix*, Fig. S5). Statistical tests found significant differences in both $\delta^{13}C_{coll}$ and $\delta^{13}C_{ap}$ when comparing Tiwanaku to the Early, Middle, and Late Formative time periods (but no differences between the Formative periods when compared to each other; *SI Appendix*, Supplementary Information Text).

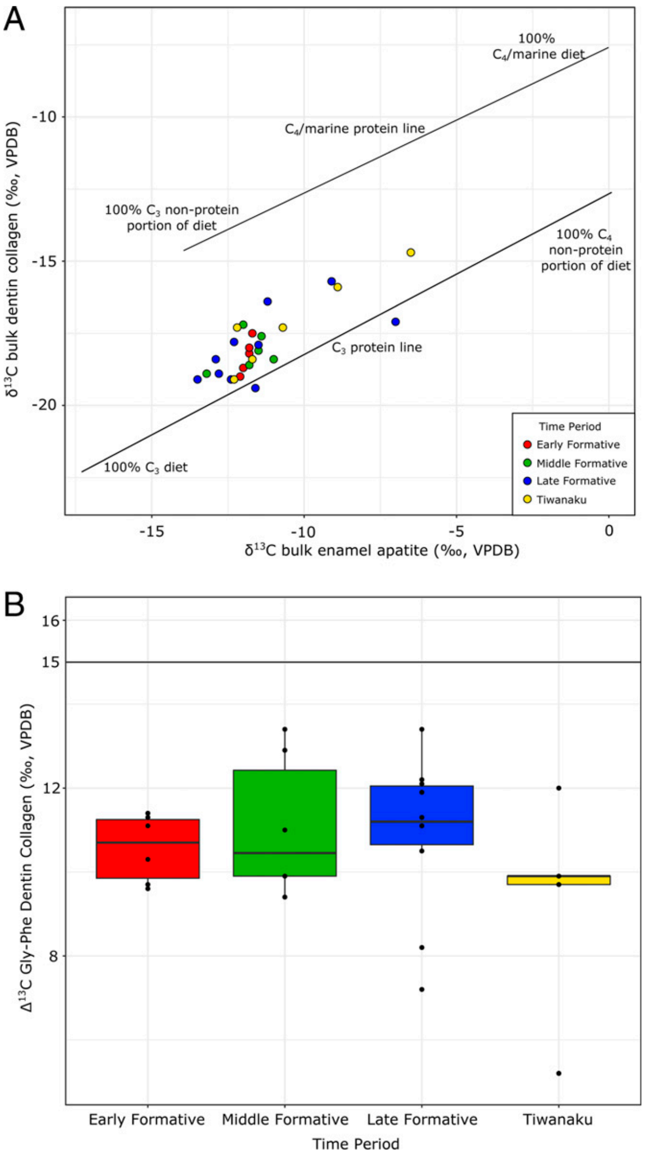

Fig. 3. (*A*) Bulk $\delta^{13}C$ enamel apatite and bulk $\delta^{13}C$ dentin collagen values for ancient humans plotted with Froehle et al. (48) dietary regression lines (*SI Appendix*, Supplemental Text). (*B*) $\Delta^{13}C_{Gly\text{-}Phe}$ values for ancient Taraco Peninsula peoples across time periods plotted with a vertical line at $\Delta^{13}C_{Gly\text{-}Phe}$ = 15‰ (values ≥15‰ indicate aquatic resource consumption).

Dentin collagen from 27 individuals was submitted to amino acid $\delta^{13}C_{AA}$ analysis (Figs. 2*B* and 3*B* and *SI Appendix*, Fig. S3 and Dataset S1). The $\delta^{13}C_{Gly}$ values range from –17.2 to –11.5‰ (average $\delta^{13}C_{Gly}$ = –14.7‰; SD = 1.6‰), $\delta^{13}C_{Phe}$ ranges from –28.3 to –21.4‰ (average $\delta^{13}C_{Phe}$ = –25.3‰; SD = 1.7‰), and $\delta^{13}C_{Lys}$ values range from –23.5 to –12.9‰ (average $\delta^{13}C_{Lys}$ = –18.9‰; SD = 2.7‰). The $\Delta^{13}C_{Gly\text{-}Phe}$ values range from 5.2 to 13.4‰ (average $\Delta^{13}C_{Gly\text{-}Phe}$ = 10.6‰; SD = 1.8‰). No human $\Delta^{13}C_{Gly\text{-}Phe}$ values are at or above 15‰, suggesting that aquatic proteins were not a major dietary component. There are no statistically significant differences between the means for each amino acid ($\delta^{13}C_{Gly}$, $\delta^{13}C_{Phe}$, or $\delta^{13}C_{Lys}$) or the calculated $\Delta^{13}C_{Gly\text{-}Phe}$ proxy across time periods (*SI Appendix*, Supplementary Information Text).

Discussion

Bulk and compound-specific stable isotope values of the plants and animals provide essential information toward creating an isoscape for the region and establishing comparative data for human dietary reconstructions (54, 65). The flora and fauna show a wide range of bulk and amino acid isotopic values, with expected patterning for C_3 and C_4 plants and anticipated trophic shifts between plants and animal consumers. The human bulk isotope values indicate diets were dominated by C_3 plants and animals consuming C_3 plants (Figs. 2 *A* and *B* and 3 *A* and *B*). In combination with archaeobotanical and zooarchaeological remains, these isotopic data verify that terrestrial domesticates, especially quinoa, tubers, and domesticated camelids, were the dominant dietary components of southern Lake Titicaca inhabitants over millennia (21, 40). In contrast to zooarchaeological evidence, however, no humans displayed $\Delta^{13}C_{Gly\text{-}Phe}$ values greater than 15‰, which is the lower cutoff for diets based on aquatic resources (53). The average $\Delta^{13}C_{Gly\text{-}Phe}$ of 10.6‰ for humans suggests that for most people, their primary dietary proteins were derived from terrestrial resources (Fig. 3*B*). Therefore, despite the ubiquitous presence of fish bones across archaeological phases and contexts on the peninsula, fish from Lake Titicaca do not appear to have been a significant dietary protein source for humans. However, three individuals (two from the Middle Formative and one from the Late Formative) have the highest $\Delta^{13}C_{Gly\text{-}Phe}$ values, around 13‰, and may have consumed more fish than others.

Over time, domesticated crops and herds persisted and intensified, suggesting that people in the southern Titicaca basin developed a reliable and stable food base that allowed sustained population growth throughout both political and climatological changes (27). Despite the availability of other accessible food sources, such as aquatic wild resources, people relied most frequently on the crops and herds they grew and cared for. More importantly, the investment by local peoples in developing and intensifying domesticated terrestrial foodways seems to have been a primary component that facilitated increased sociopolitical differentiation (21, 36). The resilience of this resource base provided the necessary fuel for population growth, surplus food production, and the expansion of communities across the southern Lake Titicaca region, laying the foundation for the development, and ultimately the spread, of the Tiwanaku polity (43).

Examining human dietary patterns over time, we observe that C_3 plants and C_3-feeding animals persist as the subsistence base, with only minor evidence of another politically important food, maize, emerging during the Tiwanaku period (Fig. 3*A* and *SI Appendix*, Fig. S5). One Late Formative individual (L7119) has a relatively elevated bulk $\delta^{13}C_{coll}$ value, possibly signaling maize consumption, which would be the first hint of this important food in human diets on the Taraco Peninsula. Within the Tiwanaku period, we see a shift in the bulk $\delta^{13}C$ values suggestive of increased maize consumption, likely as a result of the increasing social importance of maize beer in redistributive feasts, which intensified during the Middle Horizon within the Tiwanaku state (30, 33). Further, $\Delta^{13}C_{Gly\text{-}Phe}$ values <15‰ confirm that the diets of these individuals were dominated by terrestrial foods. Consequently, the dietary shift for those with higher bulk $\delta^{13}C$ values was likely driven by maize consumption, not fish.

Importantly, these isotopic data are derived from teeth, which represent the diets from specific periods of childhood/adolescence for each individual studied (*SI Appendix*, Supplementary Information Text). Diets of young people may or may not be the same as adulthood diets; children may consume the same foods as the adults around them but in different proportions and/or particular foods may be valued or discouraged based on cultural beliefs about what foods are appropriate for young people. Here, we see that while maize is being incorporated into the diets of Tiwanaku period Taraco Peninsula individuals, as evidenced by the carbon isotope shift relative to the preceding Formative periods, the amount of maize consumed by most people (at least during their youth) was still minor. Maize was clearly not being utilized as a weaning food in this community (*SI Appendix*, Supplementary Information Text), which contrasts with other areas of South America, such as north coast Peru, where longstanding use of maize, including its role in feeding children, has been documented (66). Further, the hint of maize detected in the dental isotope values for the Taraco Peninsular people studied here may underrepresent overall maize consumption for this community if maize was primarily consumed by adults (67, 68). The scarcity of maize botanical remains on the peninsula suggests it was likely imported through the Late Formative times, as it remained rarely consumed. Morphology of maize specimens coupled with major settlements in the lowland maize-growing regions during the Tiwanaku period suggests it was imported throughout that time, but it is possible that local farmers were beginning to select for the variety that grows in the region today (21, 69). Combining the limited archaeobotanical findings of maize with the minor isotopic shift found in the dental samples, we believe that it was unlikely that maize was used as a staple food for Taraco Peninsula inhabitants at any time and that maize consumption was likely limited to specific sociopolitical events.

For comparison, Berryman (33) analyzed bone collagen from Late Formative and Tiwanaku period adult individuals buried at Tiwanaku and nearby sites. She found that Late Formative diets focused on C_3 resources and that during the Tiwanaku era, maize was not uniformly consumed by those who were interred there (33). Instead, a wide range of dietary diversity was observed for Tiwanaku period peoples, where some individuals consumed a lot of maize while many others had diets primarily composed of C_3 foods, with only slight evidence of maize consumption. It is hypothesized that individuals buried at the site of Tiwanaku may not all be local to the altiplano region (33, 70), and thus some of the isotopic results may show the dietary patterns of people from distant regions who were incorporated into the Tiwanaku state (regions where maize may have easily grown and been a staple as well as a ceremonial food). The overall pattern of dietary findings between the Taraco Peninsula isotopic values presented here and those from Berryman's study (33) as well as more recent data (70) show similar trends: individuals in the Late Formative period primarily relied on C_3 resources, followed by a dietary shift in the Tiwanaku period with the incorporation of maize in varying degrees from person-to-person. Further, Berryman (33) analyzed a small number of individuals who lived after the collapse of the Tiwanaku polity and found that their diets returned to C_3-dominant isotopic signals, which implies that the consumption of maize was a unique feature for peoples who were part of Tiwanaku state practices in the Titicaca basin.

Altogether, these findings support the hypothesis that the regional altiplano dietary staples of potatoes, quinoa, and camelids were crucial in the sustained development of local populations over time and that one particular food, maize, became incorporated into sociopolitics of the Tiwanaku state without it becoming a staple food for all individuals within the Tiwanaku political sphere. Maize would have been consumed during sporadic feasting events, and differential consumption likely favored emerging political leaders on the peninsula (30, 33). Who gets to eat or drink "exotic" foods that are culturally valued, such as maize, can be an important indicator of individual and group politics, economics, and identity (1, 71).

Conclusions

While small and large-scale societies around the world have always grappled with the core issue of food security and establishing a stable resource base, it is through anthropological studies of subsistence practices in ancient communities that we can better understand the dynamic social, economic, political, and ideological roles of food security in human cultural development over time (72). Stable isotopic information from the southern Lake Titicaca basin has clarified food production and consumption practices, which centered on local, domesticated terrestrial resources and allowed for sustainable population growth and increasing political differentiation. Contrary to our expectations, fish from the lake were not a primary subsistence resource, even though in more recent times fish have served as a crucial economic and food resource, particularly for specialized groups, such as the Uru (16, 73). Instead, the lake may have been most important to local peoples for enabling increased agricultural production by creating microclimatic conditions that produced average warmer temperatures, reduced frost days, had higher average precipitation, and had overall enriched biomass. As selection and production of quinoa and tubers along with care for camelids intensified over time, this resource base took on important meanings within local communities and elites who were able to accrue surpluses to fund religious infrastructure and sponsor redistributive feasts (36, 74).

Political groups have long used foodways as drivers of economics, identity, and ideology, but how food is mobilized within these settings is highly variable. From studies of human dietary patterns completed to date, it appears that maize was important for the social and political functioning of the Andean Middle Horizon states of Wari and Tiwanaku; however, neither had universal influence in changing the diets of the communities their polities influenced (33, 67, 75–81). Our evidence from the Taraco Peninsula shows that maize was incorporated into some Late Formative and Tiwanaku period peoples' diets, but it appears to have been relatively minor or infrequent and likely relegated to special events. Despite being in close proximity to the Tiwanaku center and the lakeshore, where maize is now regularly cultivated, the people living on the Taraco Peninsula did not eat maize as a staple food. It appears that even as maize rose in prominence and value within the Tiwanaku polity, most people's diets remained reliant on locally produced staples, the same foods their ancestors had consumed for millennia.

The agropastoral products of quinoa, tubers, and camelid meat were the central features of cultural foodways that underpinned human social and political developments in the southern Lake Titicaca basin. While climate and sociopolitical structures changed over time, the foods that people regularly ate remained quite stable. Whereas the lake's rich aquatic resource of fish may not have been as important as it is today for daily subsistence, its unique microclimatic conditions, being variable, enabled the development of a highly sustainable agropastoral food system. The commitment to local, domesticated crops and herds likely developed as a long-term strategy for guaranteeing food security by maximizing stability and minimizing the inherent variability associated with agricultural risk and climatic variance. Furthermore, in the face of profound political changes, dietary practices may have been a social tie to anchor communities to their shared heritage and to resist other forms of external forces and power through (seemingly) small acts such as eating.

Materials and Methods

Sampling. Archaeological and modern botanical, faunal, and human samples for isotope analyses were collected in the context of the Taraco Archaeological Project. The results of all isotopic analyses are included in *SI Appendix*, Supplementary Information Text and Dataset S1.

Bulk Collagen and Apatite Stable Isotope Analyses. All inorganic apatite (enamel and bone) samples were prepared for carbonate analysis following published procedures using bleach and acetic acid (82). Apatite samples were analyzed at the Laboratory for Environmental and Sedimentary Geochemistry at the University of California, Berkeley (*SI Appendix*, Supplementary Information Text). Stable oxygen isotope data for the humans and animals are discussed in the *SI Appendix*, Supplementary Information Text. Most of the collagen (bone and tooth dentin) presented here was prepared at laboratories at the University of California, Berkeley and followed a modified version of the "chunk" method (83, 84). Plant (homogenized powder) and bone/tooth collagen samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ at the Center for Stable Isotope Biogeochemistry at the University of California, Berkeley (*SI Appendix*, Supplementary Information Text). Additionally, 11 camelid bone collagen samples and 10 human tooth collagen samples were prepared for radiocarbon dating at the Human Paleoecology and Isotopic Geochemistry and accelerator mass spectrometry (AMS) radiocarbon dating laboratories at The Pennsylvania State University (*SI Appendix*, Supplementary Information Text). In all cases, collagen preservation was assessed by % yield, %C, %N, and atomic C:N ratios. All collagen samples had yields greater than 5% and C:N ratios between 3.0 and 3.4, indicating good biogenic collagen preservation (85–88).

CSAA Stable Isotope Analysis. Collagen was extracted from bone prior to amino acid preparation, including filtration and gelatinization steps (84) (*SI Appendix*, Supplementary Information Text). Amino acid (AA) *N*-acetyl isopropyl ester derivatives were prepared according to established protocols (89, 90). AAs were identified by gas chromatography-flame ionization detection (GC-FID) by comparison with AA standards and quantified by comparison with a known amount of norleucine internal standard. The AA $\delta^{13}C$ values were determined by gas chromatography-combustion-isotope ratio mass spectrometry (GC-C-IRMS). Full details of the instrumental analyses and correction for added carbon can be found in *SI Appendix*, Supplementary Information Text and Fig. S6. $\Delta^{13}C_{\text{Gly-Phe}}$ values were calculated by subtracting the $\delta^{13}C$ value of phenylalanine from the $\delta^{13}C$ value of glycine ($\Delta^{13}C_{\text{Gly-Phe}} = \delta^{13}C_{\text{Gly}} - \delta^{13}C_{\text{Phe}}$) for each sample in order assess terrestrial versus aquatic environmental effects (49, 51, 53).

Data Analysis. Tests for normality, heterogeneity of variance, and subsequent parametric or nonparametric tests were utilized to compare means of isotopic data across time periods for the human samples (*SI Appendix*, Supplementary Information Text).

Data Availability. All bulk and compound-specific amino acid stable isotope data are reported in Dataset S1. All other study data are included in the article and/or supporting information.

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