The resiliency of diet on the Copacabana Peninsula, Bolivia

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ABSTRACT

Humans use dietary resources in many ways, employing varied subsistence strategies in response to local environmental fluctuations and innovative technologies. Documenting these patterns of resource use is an important part of our understanding of past societies and human relationships with the landscape, animals, and each other. In this paper, we present results from stable isotope analysis of 66 individuals buried on the Copacabana Peninsula, Bolivia, compared to a baseline of 28 modern floral and faunal samples, and explore individual and population access to certain types of food over time (3000 BCE–CE 1700). The data show that access to C_4 and lacustrine resources shifted slightly over time, especially during the Early Intermediate Period (CE 1–500). We argue that Copacabana peoples used diverse subsistence strategies to navigate fluctuating environmental and social conditions. This was not a teleological nor one-way process; rather, people made choices about food in response to environmental patterns, shifting subsistence strategies, differential ritual use of maize, or, most likely, a combination of all of the above.

1. Introduction

People have lived in the Titicaca Basin in Andean South America for millennia, using a variety of subsistence strategies to successfully occupy this highland landscape and eventually create one of the earliest Andean States, Tiwanaku (CE 500–1100). However, how people used resources over time in reaction to social and environmental changes is often difficult to delineate. In this article, we reconstruct dietary patterns using analysis of stable isotopes of carbon and nitrogen for people who lived on the Copacabana Peninsula of the Titicaca Basin over several thousand years, and contextualize them within environmental data provided by oxygen stable isotopes.

Our findings show how people used diverse resources and strategies to navigate environmental and social change over time. We identify important transitions during the Early Horizon (1000 BCE–CE1) and Early Intermediate Period (CE 1–500), key periods of agricultural change and trade network creation, just prior to state development. In

particular, we demonstrate that documented lake level changes correlated with shifts in diet, and that new subsistence strategies were often deployed in addition to, rather than in place of, previous methods. Finally, we show this was not a teleological nor one-way process, but that people continually adjusted diet and subsistence methods in response to environmental and social circumstances over 3000 years of lake basin occupation.

2. Background

2.1. The Titicaca basin

Lake Titicaca is the world's highest navigable lake at 3810 m above sea level (Fig. 1). It dominates the regional ecology, raising lakeside temperatures by as much as 8C, and provides habitats for a variety of plant, fish, amphibian, and avian species (Stanish, 2003, Miller et al., 2010, S.J. Chávez, 2012). More than 25 rivers drain into the lake, with

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the majority of inflow coming from Río Ramis, located in the northwest portion of the lake. Only one river drains from the lake, the small Río Desaguadero to the south. Thus, most lake level changes come from reduced inflow from local rivers and evaporation off the lake itself, rather than from drainage or overflow (Abbott et al., 1997, Fritz et al., 2012). Effectively, this makes the lake a closed basin (Fritz et al., 2012).

The Copacabana Peninsula divides Lake Titicaca into two parts: the larger, deeper northern portion of the lake, called Chucuito or Lago Grande, and the smaller, shallower southern portion called Wiñaymarka or Lago Pequeño. During the coldest Pleistocene periods, these lakes were fully separated (Abbott et al., 1997, Capriles et al., 2016). Despite these periodic separations, both areas of the lake support similar biomass and share many aquatic species. While the shallower waters of Wiñaymarka are slightly more hospitable for many fish and amphibian species, this smaller portion of the lake is also more susceptible to climactic shifts that can affect the reliability of resources (Miller et al., 2010).

Reconstructed lake levels, based on sediment cores from around the lake basin, show that at the beginning of the Holocene (ca. 8000 BCE), water levels were significantly lower than today (Abbott et al., 1997, Baker et al., 2005, Capriles et al., 2016, Cross et al., 2000, Weide et al., 2017). In fact, diatom species abundance from lake cores indicates that Lake Wiñaymarka was nearly dry ~6500 years ago, and began to fill around 4400 years ago (Weide et al., 2017). Since then, Lake Titicaca (and particularly Wiñaymarka) has fluctuated through four major cycles in the past 3500 years (Table 1). Around 1500 BCE, lake levels rose dramatically, followed by significant shoreline change and erosion (Abbott et al., 1997, Weide et al., 2017). Water levels oscillated between relatively deep and relatively shallow regularly for the next 1000 years, as suggested by prevalence of saline-tolerant vs freshwater plankton diatoms present in lake cores (Weide et al., 2017). The next prolonged drop in lake level began between 600 and 400 BCE, with lake levels rebounding by 200 BCE (Abbott et al., 1997, Weide et al., 2017). Another decrease in water levels occurred around CE 100 with levels starting to recover around CE 350. Lake levels dropped for a final time around CE 1100, with the lowest levels around CE 1300 and rebounded

to modern levels shortly thereafter (Abbott et al., 1997, Cross et al., 2000). Modern lake levels are significantly higher than they have been for the majority of the last 6000 years (Weide et al., 2017).

Throughout these lake level changes, people have lived in the Titicaca Basin of Bolivia and Peru. They used diverse subsistence strategies over time, including fishing, foraging, and agropastoralism (Bandy, 2004; Janusek, 2008; Lee, 1997; Norr, 2002; Pearsall and deFrance, 2002). During the Late Preceramic VI (3000–1000 BCE; Table 1), Titicaca Basin foragers relied on wild deer and camelids, lake resources such as fish and aquatic plants, and wild crops, and moved regularly throughout the lake basin and into lower regions (Capriles et al., 2016, Haas and Viviano Llave, 2015). While wild game was crucial to Late Preceramic diets, dental analyses from the northern lake basin showed wild tubers also played an important role (Watson and Haas, 2017). By the end of the Preceramic, people in the Titicaca Basin were in the process of domesticating camelids, supplementing their otherwise wild diet (Aldenderfer, 1989, 2005). The robust and tall people who inhabited the lake basin at that time successfully used the landscape and were well adapted to living in this region (Juengst et al., 2017a).

In the Early Horizon (hereafter referred to as EH) (1000 BCE–CE1), household-level cultivation of plants combined with foraging, hunting, herding, and fishing was associated with the establishment of sedentary settlements (Bandy, 2004, Bruno and Whitehead, 2003, Capriles et al., 2014, Moore, 2011, Moore et al., 2007). Some of the first plant domesticates included quinoa (Bruno and Whitehead, 2003) and tubers such as potatoes and oca (Aldenderfer, 1989). Lake levels fluctuated several times during this period as described above (Abbott et al., 1997); throughout these changes, large quantities of fish remains were present at lake basin sites (Capriles et al., 2014, Miller et al., 2010, Moore et al., 1999). In addition to the animal resources that the lake provided, totora reeds may have been plentiful, gathered for consumption and construction of rafts, houses, and other structures. However, it should be noted that estimates for when and how people used totora reeds are largely based on ethnographic and ethnohistoric research (e.g., Janusek, 2008, Orlove, 2002).

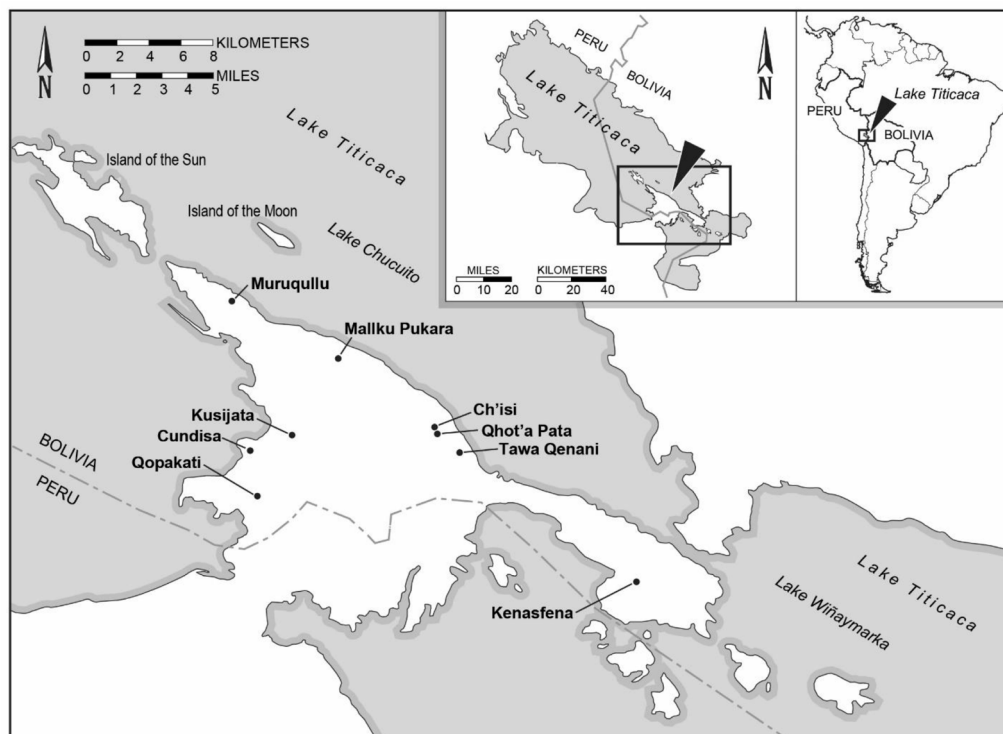By the Early Intermediate Period (hereafter referred to as EIP) (CE

Fig. 1. Map of the Copacabana Peninsula and relevant archaeological sites. Map drawn by Susan Brannock-Gaul.

Table 1
Chronology of the Titicaca Basin, associated material culture, and lake levels.

Absolute Chronology	Relative Chronology	Titicaca Basin Chronology	Associated Culture	Lake Levels (based on lake cores)
CE 1540–1800	Colonial Period (COL)	Colonial Period	Spanish	Very High
CE 1450–1540	Late Horizon (LH)	Late Horizon	Inka	High
CE 1100–1450	Late Intermediate Period (LIP)	Altiplano/Pacajes Period	Lupaka and Colla	Low
CE 500–1100	Middle Horizon (MH)	Middle Horizon	Tiwanaku	High
CE 1–500	Early Intermediate Period (EIP)	Late Formative Period	"Late" Yaya-Mama	Very Low CE 100–350
1000 BCE – CE 1	Early Horizon (EH)	Early and Middle Formative Period	"Early" Yaya-Mama	Fluctuating: High 1000-600BC, Low 600–400 BCE, High 400 BCE – CE1
3000–1000 BCE	Late (Cotton) Preceramic VI	Initial Period	Viscachani	Very High

1–500), people in the lake basin built terraced field complexes and civic architecture, grew domesticated crops, herded camelids, and established long-distance trade relationships (Bandy, 2004, Bruno and Whitehead, 2003, K.L.M. Chávez, 1988, S.J. Chávez, 2004a, 2012, Levine et al., 2013, Roddick and Hastorf, 2010, Stanish et al., 2002). While lake resources continued to be important, plant domesticates—especially quinoa and the newly introduced maize—became more common in the lake basin (Bruno and Whitehead, 2003, Chávez and Thompson, 2006, Murray, 2005, Stanish, 2003, Whitehead, 1999). Central to the regional integration of the period was a ritual tradition known as Yaya-Mama (K. L.M. Chávez, 1988, S.J. Chávez, 1976, Chávez & Chávez, 1970, 1976). Marked by semi-subterranean temples, carved stone stelae, and religious paraphernalia such as ceremonial burners, fancy and utilitarian vessels, and ceramic trumpets, Yaya-Mama temples were the earliest public architecture in the region (K.L.M. Chávez, 1988, S.J. Chávez, 2004b, 2018, Hastorf 2003).

While agricultural investment increased during the EH and EIP, the impacts of environmental and social changes on diet and subsistence practices remain unclear. How did shifting social and physical environments affect the ways people accessed resources? Were resources shared broadly across groups, or did emerging social institutions (such as public ritual) limit access to exotic goods? Did lake levels influence the inclusion of lake resources in the diet, or were other social factors driving dietary composition for groups and individuals? In order to address these questions, we report dietary and environmental isotopic data from individuals buried in seven mortuary contexts on the Copacabana Peninsula in the southern Lake Titicaca basin. They range in date from the Late Preceramic period, between 3000 BCE and 1000 BCE, through post Yaya-Mama contexts between AD 500 and 1700. We employ stable isotope analysis of carbon, nitrogen, and oxygen for 66 individuals excavated from seven sites on the Copacabana Peninsula and for 28 modern faunal and floral samples to establish an isotopic baseline for comparison.

2.2. Stable isotope dietary analysis (carbon and nitrogen)

Stable isotope dietary analysis provides direct evidence of what types of plants and animals were consumed, as many foods have distinct ratios of the stable isotopes of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$). Stable isotope ratios are a representation of the heavier to lighter isotope ratio in a sample, relative to that ratio in the appropriate standard. Expressed as delta (δ) values in parts per thousand (‰), carbon and nitrogen isotope ratios are calculated using reference standards as: $\delta^{13}C$ (‰) = $[(^{13}C/^{12}C_{sample}/^{13}C/^{12}C_{VPDB}) - 1] \times 1000$ and $\delta^{15}N$ (‰) = $[(^{15}N/^{14}N_{sample}/^{15}N/^{14}N_{AIR}) - 1] \times 1000$. When foods are eaten, the isotopic composition of the diet is incorporated into body tissues, such as bone collagen and apatite (Ambrose, 1993, Ambrose and Norr, 1993, Katzenberg, 2008, Lee-Thorp, 1986, Schoeninger and Moore, 1992).

The variation in the carbon isotope composition of the terrestrial foods we eat is a result of differential fractionation among the C_3, C_4, or CAM (Crassulacean Acid Metabolism) photosynthetic pathways (Smith and Epstein, 1971, Troughton et al., 1974). Plants using the C_3 photosynthetic pathway discriminate strongly against ^{13}C in atmospheric CO_2 during uptake, resulting in stable carbon isotope ratios that average − 26.5‰ compared to C_4 plants, which discriminate to a lesser degree against the heavy isotope, and that average − 12.5‰. Most temperate plants are C_3 photosynthetic pathway plants, such as trees, shrubs, and temperate and high altitude grasses (Smith and Epstein, 1971, Troughton et al., 1974, Farquhar et al., 1989). Maize and related tropical grasses are the major New World C_4 food plants. The CAM plants are able to shift between C_3 and C_4 photosynthetic pathways depending on their environmental conditions and include succulents such as cacti, agaves, and pineapple, among others.

Nitrogen isotopic variation reflects source nitrogen and trophic levels in marine and terrestrial environments (Capone and Carpenter, 1982, Hedges and Reynard, 2007, Keegan and DeNiro, 1988, Létolle, 1980, Schoeninger et al., 1983, Virginia and Delwiche, 1982, Wada et al., 1975). As in carbon, some plants that are important dietary items have very specific nitrogen isotopic values, such as legumes (e.g., beans) that typically obtain nitrogen directly from the atmosphere ($\delta^{15}N = 0$‰) via fixation by symbiotic bacteria. Most other terrestrial plants obtain nitrogen through assimilation of more ^{15}N-enriched soil. A trophic level enrichment from diet to consumer is estimated to be 2–3‰ (DeNiro and Epstein, 1981, Hare et al., 1991, Minagawa and Wada, 1984, Schoeninger and DeNiro, 1984); however, more recent studies suggest increases up to 6‰ may be appropriate (O'Connell et al., 2012).

Controlled diet studies allow us to interpret the relationships between dietary substrate and consumer values (e.g., Ambrose, 2000, Ambrose and Norr, 1993, Howland et al., 2003, Jim et al., 2004, Tieszen and Fagre, 1993). They demonstrate that the carbon in bone mineral apatite carbonate ($\delta^{13}C_{ca}$) accurately reflects whole diet (proteins, fats, and carbohydrates) while the carbon in bone collagen ($\delta^{13}C_{co}$) reflects mostly, but not only, the isotopic composition of dietary protein. Carbohydrate sources with distinct isotopic values, such as maize, can be identified by examining the relationship between dietary proteins and carbohydrates represented by the difference in $\delta^{13}C$ values between bone apatite carbonate ($\delta^{13}C_{ca}$) and collagen ($\delta^{13}C_{co}$), represented as $\Delta^{13}C_{ca\text{-}co}$.

Ambrose and Norr (1993) found in controlled diet studies of rodents that small differences in $\Delta^{13}C_{ca\text{-}co}$ (1–3‰) result from less negative dietary protein than the carbohydrates consumed. Large differences in $\Delta^{13}C_{ca\text{-}co}$ (8–11‰) occur when dietary protein is more negative than the carbohydrates consumed. When the isotopic composition of carbohydrates and protein are similar, the $\Delta^{13}C_{ca\text{-}co}$ values are intermediate (5–7‰).

These regularities from feeding experiments can be applied to humans. The smaller $\Delta^{13}C_{ca\text{-}co}$ values occur when a marine protein is consumed with tubers, nuts, palm fruits, and other C_3 plants. Large differences in $\Delta^{13}C_{ca\text{-}co}$ are indicative of a terrestrial protein, such as deer and small mammals, combined with C_4 plants, such as maize, and/or CAM plants, such as prickly pear. Intermediate $\Delta^{13}C_{ca\text{-}co}$ values (5-7‰) indicate either a highly mixed diet of marine and terrestrial

proteins and C_3, C_4, and CAM plants, or a monoisotopic diet where protein and energy sources are isotopically similar.

In addition to Ambrose and Norr's (1993) study, a number of other studies have examined the relationship of foods consumed as compared to the isotopic values they yield in tissue. One point of discussion has been the mammalian experimental model used in controlled diet experiments: rodents or pigs. Most studies (Ambrose and Norr, 1993, Jim et al., 2004, Tieszen and Fagre, 1993) have used rodents (*Mus musculus* and *Rattus norvegicus*). Critics of those studies argue that there are extensive differences between larger terrestrial mammals and rodents in digestive physiology, metabolic rate, and feeding habits. The critics have used pigs, which are more similar in those variables to humans (Howland et al., 2003, Warinner and Tuross 2009).

Several further studies (Froehle et al. 2010; Froehle et al., 2012; Kellner and Schoeninger 2007; Warinner and Tuross 2009) refined the translation of stable isotope values obtained from consumer tissues, particularly those of carbon, to consumer diet. They have demonstrated the complex relationship between diet, food preparation methods, and eventual consumer isotopic values. We highlight particularly the methods for accurate dietary reconstruction provided by Froehle et al. (2012), who formulated a multivariate diet reconstruction model that incorporates $\delta^{13}C_{ca}$, $\delta^{13}C_{co}$, and $\delta^{15}N$. They incorporate archaeological human data and generate five cluster centroids: (1): 100% C_3 diet/protein, (2): 30:70 C_3:C_4 diet, >50% C_4 protein, (3): 50:50 C_3:C_4 diet, marine protein, (4): 70:30 C_3:C_4 diet, >65% C_3 protein, and (5): 30:70 C_3:C_4 diet, >65% C_3 protein. The functions resulting from their multivariate model can be applied to new cases, allowing them to be plotted against the Froehle et al. (2012) cluster centroids.

2.3. Stable isotope climate analysis (oxygen)

Oxygen isotopes ($^{18}O/^{16}O$) vary because of atomic weight and a number of environmental factors, including rainfall, temperature, and elevation. Lighter isotopes (^{16}O) evaporate more readily, and are thus more common in areas of low evaporation, while heavier isotopes (^{18}O) precipitate more readily as rainfall but are slower to evaporate. Oxygen isotope data is expressed as $\delta^{18}O$, comparing the isotopic ratio of the sample to that of a standard (i.e., $\delta^{18}O = (((^{18}O/^{16}O_{sample})/(^{18}O/^{16}O_{standard})) - 1) \times 1000$) (Craig, 1961b, Coplen, 1994). Standard values are normalized using both VSMOW (Vienna Standard Mean Ocean Water) and SLAP (Standard Light Antarctic Precipitation) standards on the VSMOW/SLAP scale (Coplen, 1995, 1996, 2011, Craig, 1961a,b). Sample values are often reported on the VPDB (Vienna Pee Dee Belemnite) scale and values can be related to each other using a conversion established by Coplen et al. (1983): $\delta^{18}O_{VSMOW} = (1.03091 \times \delta^{18}O_{VPDB}) + 30.91$.

Oxygen isotopes are incorporated into the phosphate and carbonate in hydroxyapatite in human bone and dental enamel, reaching equilibrium in $\delta^{18}O$ between body water and consumed water. Building on studies in the natural sciences, archaeologists and bioarchaeologists have used oxygen isotopes to track human and animal migration, and reconstruct climate variations for a region over time (see Buzon and Bowen, 2010, Knudson, 2009, Knudson and Price, 2007, Knudson et al., 2012, Reinhard et al., 1996, Turner et al., 2009, White et al., 2007). Studies have shown that oxygen phosphate and oxygen carbonate resist diagenetic contamination (although risk of contamination increases in fossilized samples and with heating above 300) (Lee-Thorp, 2002, Lee-Thorp & van der Merwe, 1991, Lee-Thorp & Sponheimer, 2003, Nelson et al., 1986, Sharp et al., 2000). While some oxygen phosphate and carbonate may stem from inhaled oxygen, the majority comes from imbibed water or from water in food sources (Longinelli, 1984, Luz et al., 1984, Luz & Kolodny, 1985).

Generally, $\delta^{18}O_{mw}$ (meteoric water) decreases with elevated altitude, latitude, and distance from the coast, and decreased temperature (Bowen & Wilkinson, 2002, Craig, 1961b, Knudson, 2009, Koch, 1998, Pederzani & Britton, 2019). However, several other factors influence the oxygen ratios in these water sources. First, there is variation between groundwater and precipitation-based systems. Groundwater systems, such as lakes, rivers, and cisterns may have $\delta^{18}O$ values that indicate more ^{18}O depleted sources, if their influx of water comes from higher elevations, where lighter isotopes tend to dominate. However, these systems may also be susceptible to evaporation depending on size, leaving behind the heavier isotopes. Precipitation-based systems may fluctuate more rapidly in response to seasonality or other shifts in weather patterns (Darling et al., 2003, Gat, 1995, Gibson et al., 2016, Kendall and Coplen, 2001, Knudson, 2009, Pederzani & Britton, 2019, Tian et al., 2001, van Geldern and Barth, 2016).

Additionally, storage and preparation (i.e., boiling) of water may change $\delta^{18}O$ values, as ^{16}O evaporates more readily during both processes (Gagnon and Juengst, 2019, Knudson, 2009, Wilson et al., 2007). Finally, breastfeeding may change values for young individuals, as $\delta^{18}O$ values from body water are enriched in ^{18}O compared to imbibed water (Roberts et al., 1988). Thus, interpretations of oxygen isotope data should occur with an understanding of the archaeological context and in conjunction with other isotopic studies to delineate potential dietary factors.

2.4. Isotope studies in Andean South America

In Andean South America, (bio)archaeologists use stable isotopes of carbon and nitrogen to show major dietary shifts over time (i.e., Finucane et al., 2006, Finucane, 2009, Goldstein, 2003, Hastorf, 1985, 1991, Kellner and Schoeninger, 2007, Sanhueza & Falabella, 2012, Tung and Knudson, 2018, Turner et al., 2018), and dietary variation within groups (i.e., Burger and van der Merwe, 1990, Somerville et al., 2015, Tung et al., 2016, Williams and Katzenberg, 2012). Oxygen isotopes facilitate interpretations of individual and population movements (i.e., Barberena et al., 2017, Knudson, 2009, Knudson and Price, 2007, Knudson and Tung, 2011, Turner et al., 2009), and paleoclimates (i.e., Knudson, 2009, Wolfe et al., 2001).

There are two main challenges to isotope analyses in the Andes. The first involves the fact that Andean diets included multiple plants using the C_4 photosynthetic pathway, a phenomenon that occurs in other parts of the world as well. Researchers address that challenge by combining isotopic dietary reconstruction with archaeological evidence of plant remains. While maize was considered the only Andean C_4 plant for many years, Cadwallader et al. (2012) demonstrated that many edible species of amaranth might also contribute to more positive $\delta^{13}C$ signatures, either through direct human consumption or through animal foddering. Thus, investigations of Andean diet should not assume a direct correlation between increasing $\delta^{13}C$ and maize consumption, but must incorporate archaeobotanical data on available wild and domesticated plants.

The second challenge in Andean stable isotope analysis is unrelated to diet but important for understanding oxygen isotopes. Because of the vertical landscape of the Andes and the circulation of water and people through this landscape, oxygen isotopes are not always the most reliable source of data on migration. In the Andes, oxygen isotopes often have an "averaged" effect, as they reflect movement of water (and people) through different elevations and environmental zones (Knudson, 2009). While this makes oxygen isotopes less useful for tracking migrations, it still possible to use these data to reconstruct local environments, especially near a relatively circumscribed body of water, such as a lake (Knudson, 2009, Wolfe et al., 2001).

3. Materials and methods

In order to reconstruct the diet of the Copacabana Peninsula populations, we analyzed the stable isotope ratios of carbon and nitrogen from 66 individuals (Table 2). We also analyzed oxygen isotopes for those same individuals in order to understand how variation in environmental conditions may have affected both diet and isotopic dietary

Table 2
Age and Sex distribution across time periods (PC = Preceramic, EH = Early Horizon, EIP = Early Intermediate Period, MH = Middle Horizon, LIP = Late Intermediate Period, COL = Colonial).

	Female	Indeterminate Adult	Male	Juvenile	Total
Preceramic	1	0	5	1	7
EH	7	3	5	6	21
EIP	5	1	13	2	21
MH	3	3	0	5	11
LIP	1	1	1	0	3
COL	1	0	2	0	3
Total	18	8	27	13	66

signatures. Human bone samples were selected based on presence of duplicated elements or elements of less analytical value. We selected samples from a range of demographic categories and temporal periods to capture as much variation as possible.

Our sample included 53 adults and 13 juvenile individuals (under 15 years of age at the time of death). Twenty-seven individuals were classified as males, 18 as females, and 21 as of indeterminate sex. With regard to temporal span, seven samples were from Preceramic (3000–1000 BCE) contexts, 21 from the EH (800 BCE–CE1), 21 from the EIP (CE 1–500) contexts, 11 from Middle Horizon (CE 500–1100) contexts, three from Late Intermediate Period (CE 1100–1450) contexts, and three from Colonial contexts (CE 1540–1800) (Table 2). Samples analyzed in this study were collected and analyzed in two different batches at the University of Florida. Samples with prefix 'dh' were run in 1999 and samples with prefix 'sj' were run in 2018.

All bone samples were prepared for collagen extraction by methods previously described by Ambrose (1990) and for apatite extraction by methods previously described by Lee-Thorp (1986). Collagen was isolated following methods described in Ambrose (1990). Briefly, 1–2 g of archaeological bone was cleaned, dried, and ground to between 0.25 and 0.50 mm. Bone samples were demineralized in 0.2 M HCl and rinsed to neutrality before treatment with 0.125 NaOH to remove humic and fulvic acids and then again rinsed to neutrality. After this step, the organic solutions were then solubilized in 10–3 M HCl at 95 °C, cooled and then lyophilized (freeze-dried).

Isotope ratios for 'dh' collagen samples were measured on a Finnigan-MAT DeltaPlus XL isotope ratio mass spectrometer (IRMS) and a Costech ECS 4010 CHNSO elemental analyzer. 'SJ' samples were measured on a Delta V IRMS and a Carlo-Erba NA1500 CNS elemental analyzer. Collagen C:N ratios ranged between 3.2 and 3.5, indicating well-preserved collagen with no noticeable contamination, with the exception of five individuals which dod not yield collagen (Table 5) (Ambrose, 1990, DeNiro, 1985).

Bone apatite carbonate was extracted from approximately 100 mg of clean, dry, archaeological bone ground to a powder of less than 0.25 mm following the methods of Lee-Thorp (Lee-Thorp, 1989, Lee-Thorp et al., 1989). Briefly, organic matter was removed from the bone powder in centrifuge tubes with a 50:50 (~2.5%) sodium hypochlorite solution, rinsed to neutrality, treated with a 0.5 M acetic acid to remove diagenic carbonates, and neutralized again. Samples were then frozen and lyophilized, and after loading, converted to CO_2 by reaction with 100% phosphoric acid (H_3PO_4) at 90 °C for 25 min using a Kiel carbonate prep device. Samples with a 'dh' prefix were measured on a Micromass PRISM IRMS and samples with a 'sj' prefix were measured on a Finnigan MAT 252 IRMS.

All but the previously mentioned five human bone samples yielded interpretable results for nitrogen and carbon from organic collagen based on the ratio of carbon to nitrogen (C:N) in the collagen sample (DeNiro, 1985) (Table 5). With respect to the apatite carbon samples, all 'dh' samples were assessed for quality using % wt. carbon following Ambrose et al. (1997) and all 'sj' samples assayed produced excellent results. For the 'sj' samples, precision of USGS40 standards (n = 13) was 0.040 for $\delta^{15}N$ and 0.052 for $\delta^{13}C$ and for NBS-19 standards (n = 12) was

0.025 for $\delta^{13}C$ and 0.049 for $\delta^{18}O$.

Modern floral and faunal samples were collected by Karen Mohr Chávez and Sergio Chávez from traditional rural farming communities on the Copacabana Peninsula, to make sure samples were not contaminated with chemical pesticides, insecticides, fertilizers and/or derived from commercial markets. The only product which came from outside the region were the coca leaves, which we obtained from local villagers who got them from their relatives working in the coca-growing regions of lower Cochabamba in Bolivia. These leaves were grown for personal consumption, rather than commercial sale, and were not treated with chemicals.

All plant and animal samples were modern edible portions, which were cleaned and rinsed in distilled water before freeze-drying and grinding in a Wiley-Mill. Carbon and nitrogen were assessed by the same methods as the 'dh' human bone. The resulting carbon isotopic values were adjusted by 1.5–compensate for the increased relative abundance of ^{12}C in the modern atmosphere (the Suess effect; Keeling et al., 1979, Marino and McElroy, 1991).

In order to compare human isotope values with those obtained from modern plants and animals, some conversions for the human isotope values are required. The average isotopic composition of human diet is reconstructed from human bone collagen $\delta^{15}N$ values, adjusted downward by 3.0‰ to account for the trophic level effect (DeNiro and Epstein, 1981, Koch, 1998, Norr, 1995), and from apatite carbonate $\delta^{13}C$ minus 9.5‰ to account for fractionation between diet and bone carbonate (Ambrose and Norr, 1993, Lee-Thorp et al. 1989, Tieszen and Fagre, 1993). The 9.5‰ adjustment is largely based on controlled diet experiments with rodents; higher offsets have been demonstrated in controlled feeding experiments with pigs of 12-13‰ (Howland et al., 2003, Warinner and Tuross 2009).

4. Results

The results of the stable isotope analysis are presented here, in Figs. 2–10, and Tables 3–5. Table 3 shows the results of the modern faunal and floral samples, which we use as a comparative baseline for the human tissue samples. Table 4 shows the average results and differences between males and females for each period, while Table 5 details the results for each sampled individual.

Modern faunal and floral samples resulted in a comparative baseline for the human samples (Fig. 2, Table 3). Carbon from human apatite and collagen indicated a generally mixed diet of lacustrine and terrestrial resources with limited inclusion of C_4 plants throughout all periods
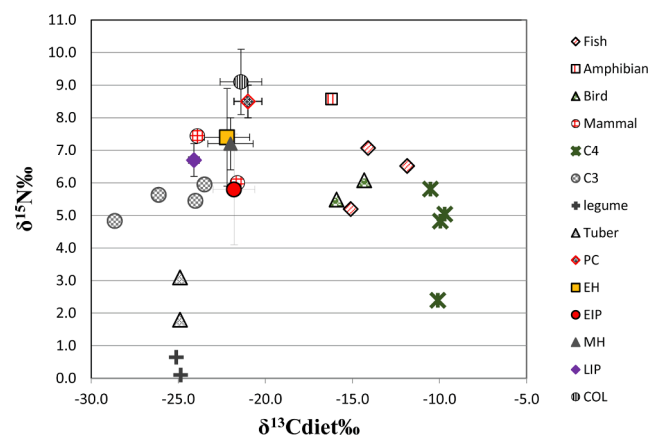
Fig. 2. Dietary isotopic results. Modern plant and animal samples with human mean values by time period. Human mean error bars are one standard deviation. There are two outlying plant data points not shown on this plot, DH384 (coca; $\delta^{13}C = -30.2$, $\delta^{15}N = 4.8$) and DH 375 (Tarwi; $\delta^{13}C = -23.8$, $\delta^{15}N = -0.1$). (PC = Preceramic, EH = Early Horizon, EIP = Early Intermediate Period, MH = Middle Horizon, LIP = Late Intermediate Period, COL = Colonial).
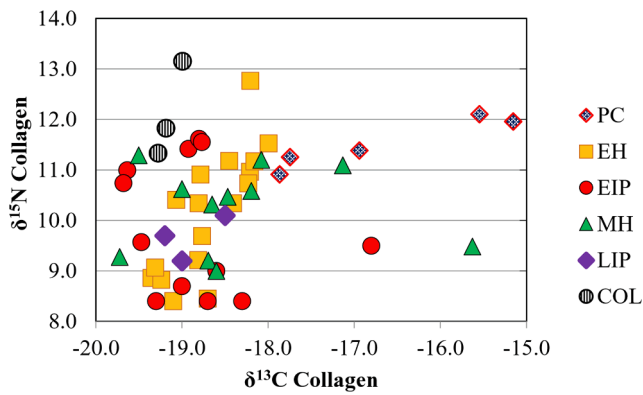
Fig. 3. Distribution of δ^{13}C collagen values across time periods. (PC = Preceramic, EH = Early Horizon, EIP = Early Intermediate Period, MH = Middle Horizon, LIP = Late Intermediate Period, COL = Colonial).
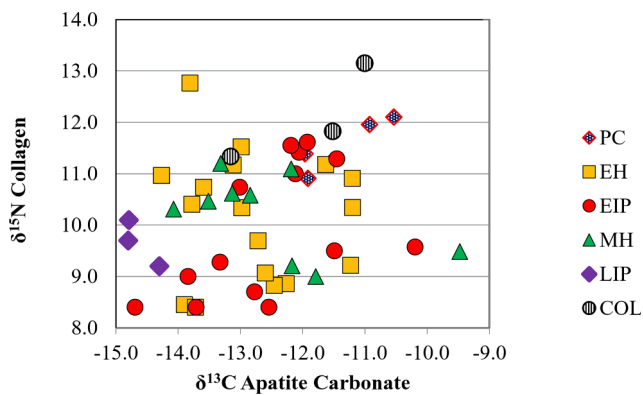

Fig. 4. Distribution of δ^{13}C apatite carbonate values across time periods. (PC = Preceramic, EH = Early Horizon, EIP = Early Intermediate Period, MH = Middle Horizon, LIP = Late Intermediate Period, COL = Colonial).
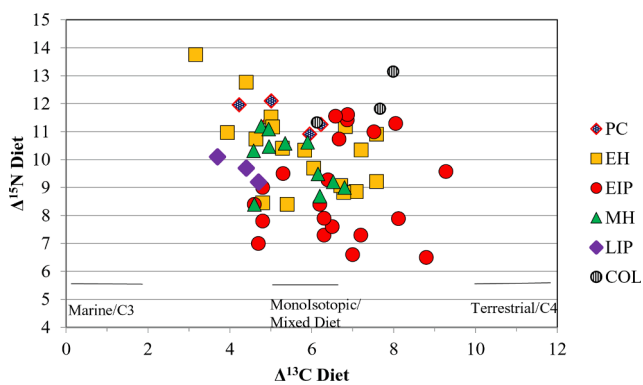

Fig. 5. Distribution of carbon spacing values across all samples plotted above dietary interpretations from Ambrose and Norr (1993). (PC = Preceramic, EH = Early Horizon, EIP = Early Intermediate Period, MH = Middle Horizon, LIP = Late Intermediate Period, COL = Colonial).

when plotted against our modern plant and animal values and standards established by Ambrose and Norr (1993) (Figs. 2–5; Tables 4 and 5). When compared with functions as described by Froehle et al. (2012), our values cluster closely with centroid 4 (70:30 C$_3$:C$_4$ diet, >65% C$_3$ protein) and centroid 1 (100% C$_3$ diet/protein) (Fig. 6). When plotted along dietary estimation regression lines as established by Froehle et al. (2010, following Kellner & Schoeninger, 2007), our data cluster along the C3 protein line.
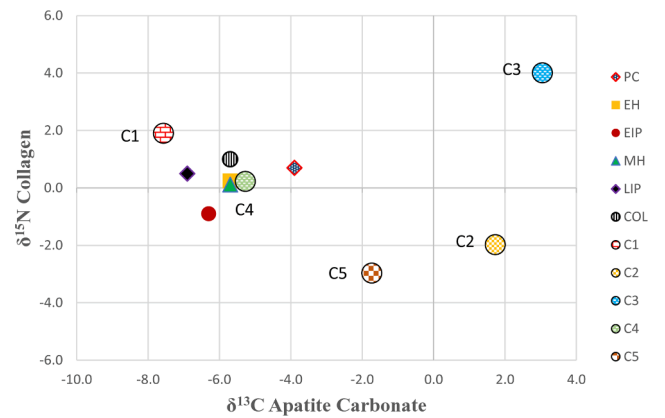

Fig. 6. Distribution of average δ^{13}C apatite carbonate values for each time period compared to K-means cluster centroids for dietary estimation developed by Froehle et al. (2012). (PC = Preceramic, EH = Early Horizon, EIP = Early Intermediate Period, MH = Middle Horizon, LIP = Late Intermediate Period, COL = Colonial; C1-C5 indicate the five clusters from Froehle et al. 2012).
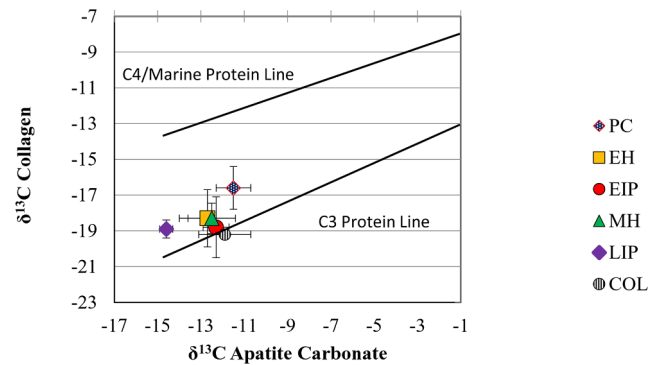

Fig. 7. Bivariate plot of mean carbon apatite and collagen isotope values for all time periods, compared to regression lines for dietary estimation from Froehle et al. (2010:2669) following Kellner and Schoeninger (2007). (PC = Preceramic, EH = Early Horizon, EIP = Early Intermediate Period, MH = Middle Horizon, LIP = Late Intermediate Period, COL = Colonial).

In order to investigate the differences in isotopic values by period, we employed one-way ANOVA when normal distributions were indicated by Lilliefor's Test for normality (Lilliefors, 1967). Carbon collagen and nitrogen values had abnormal distributions; we employed nonparametric Kruskal-Wallis tests for these measures instead (Harris, 1985). The assumption of equal variances was determined using Levene's test, which indicated all samples met the requirement of equal variance (Brown & Forsythe, 1974). Both the ANOVA and Kruskal-Wallis tests indicate when there are significant differences between groups, but not which group is different. For those dependent variables that exhibited significant differences, we employed notched box plots to help identify the significant outlier.

Colonial (hereafter referred to as COL) samples reflected the most reliance on terrestrial and C$_4$ resources, both plant and animal, and the highest nitrogen values, suggesting the most meat consumption. Late Intermediate Period (hereafter referred to as LIP) and Middle Horizon (hereafter referred to as MH) samples had the least positive carbon apatite values (δ^{13}C$_{ap}$) and the narrowest carbon spacing (Δ^{13}C$_{ca-co}$), suggesting the least reliance of C$_4$ resources and a diet of marine resources and C$_3$ plants. Δ^{13}C$_{ca-co}$ was a statistically significant difference, based on ANOVA statistical tests (F (5, 55) = 2.980, p = .019), with LIP and COL group values as outliers.

Carbon apatite differences were also statistically significant based on ANOVA statistical tests (F (5, 60) = 3.186, p = .013), with the LIP group
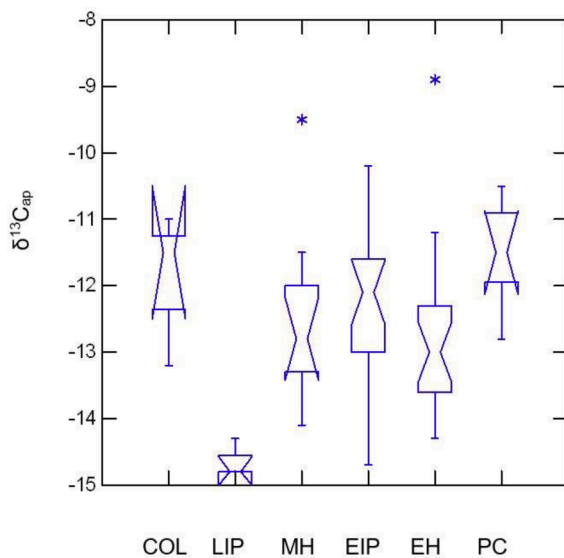
Fig. 8. Notched box plot of $\delta^{13}C$ apatite carbonate values by time period. Note the deviation during the LIP. The MH outlier is sj3, and the EH outlier is sj25. (PC = Preceramic, EH = Early Horizon, EIP = Early Intermediate Period, MH = Middle Horizon, LIP = Late Intermediate Period, COL = Colonial).

Fig. 10. Line chart of means for $\delta^{18}O_{ap}$ by Time Period. Horizontal line between bars intersects at the mean; Vertical bars display standard error of the mean. (PC = Preceramic, EH = Early Horizon, EIP = Early Intermediate Period, MH = Middle Horizon, LIP = Late Intermediate Period, COL = Colonial).

as the significant outlier (Fig. 8). EIP samples had the lowest nitrogen values, indicating the least protein consumption, a statistically significant difference based on the Kruskal-Wallis statistical test ($\chi 2 (5) = 21.907$, $p = .001$). Preceramic individuals were outliers for carbon collagen values according to a Kruskal-Wallis statistical test ($\chi 2 (5) = 15.839$, $p = .007$). Finally, EH individuals were not statistically different from other groups, but generally had values that reflected mixed diets of C_3 and C_4 plants, and lacustrine and terrestrial protein sources. There were no statistically significant differences between males and females during any period as determined by T-tests. There were significant outliers from each period as determined by notched box plots (Table 5).

Oxygen values were consistent with baseline oxygen values reported in Knudson (2009), including Lake Titicaca surface water ($\delta^{18}O_{mw(V-}$

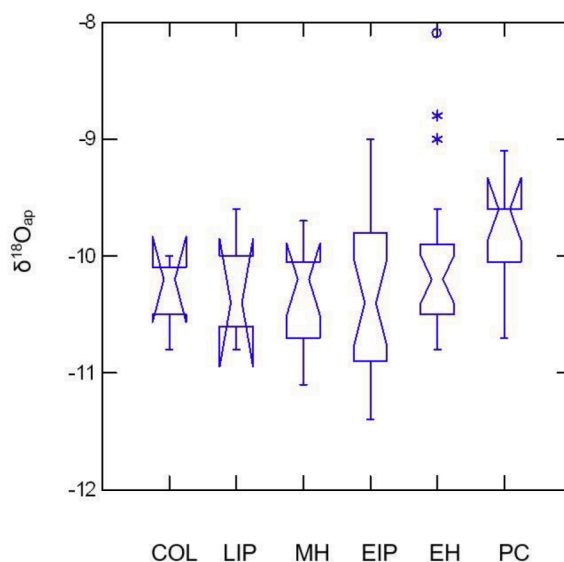**Fig. 9.** Notched Box Plot of $\delta^{18}O_{ap}$ by Time Period. Note the wide range during the EIP, and non-overlap of PC median. The EH outliers are sj30, dh127, and dh198. (PC = Preceramic, EH = Early Horizon, EIP = Early Intermediate Period, MH = Middle Horizon, LIP = Late Intermediate Period, COL = Colonial).
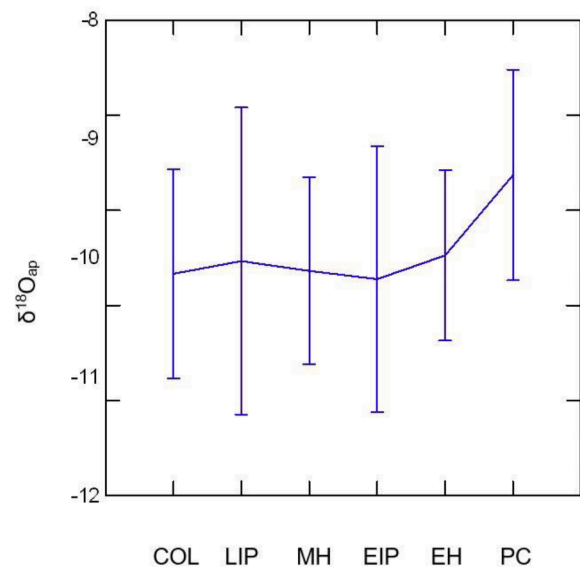
SMOW) $= - 17.6‰ - -12.6‰$), and precipitated water from La Paz ($-13.3‰ - -10.8‰$), Puno ($-18.6‰ - -8‰$), and Isla Taquile ($-22.1‰ - -12.8‰$). The lowest $\delta^{18}O$ values, suggesting high evaporation and low precipitation came from some EIP individuals, although this period overall showed a wide range of values (Figs. 9 and 10). Meanwhile, the highest values, indicating low evaporation and high precipitation, were from the Preceramic samples (Figs. 9 and 10, Tables 4 and 5). The Preceramic $\delta^{18}O$ box plot notch does not overlap with others, suggesting at a 95% confidence interval that their medians are significantly different (Fig. 9) (Chambers et al., 1983:62). Overall, there were no statistically significant differences in $\delta^{18}O$ values between different periods based on ANOVA tests ($F (5, 60) = 1.115$, $p = .362$).

5. Discussion

5.1. Diet, Environment, and social change in the Titicaca basin over time

5.1.1. Preceramic

Preceramic foragers have high nitrogen signatures, consistent with (bio)archaeological evidence for their hunting wild game and collecting wild lake resources (Juengst et al., 2017a). High protein consumption could have stemmed from both hunting and fishing. These individuals also have the lowest carbon collagen values, a pattern that highlights a statistically significant difference from other time periods, according to a Kruskal-Wallis statistical test ($\chi 2 (5) = 15.839$, $p = .007$). Carbon in bone collagen disproportionately represents carbon in the protein portion of diet (Lee-Thorp et al. 1989); this implies that PC protein sources consumed more C_4 resources than protein sources in other time periods. This is also apparent in comparison with the dietary centroids established by Froehle et al. (2012); the PC mean is the only mean less negative than centroid 4, indicating PC peoples were eating more C_4-sourced carbon from the protein provided by either animal or plants (Fig. 6).

Notably, Miller et al. (2010) report a uniquely wide range of isotopic signatures for modern aquatic plants (and fish feeding on those plants) from Lake Wiñaymarka. Our modern flora included one aquatic plant (totora) which had a relatively depleted $\delta^{13}C$ signature ($-22.9‰$), but Miller et al. (2010:323) demonstrate that some aquatic plants contribute more enriched $\delta^{13}C$ signatures. In fact, some water plants and algae are more ^{13}C-enriched than maize and amaranths. Fish feeding on these lake

Table 3

Stable Isotope Values for Modern Lake Titicaca Region Flora and Fauna. All samples from "Copacabana" came from local communities on the Copacabana Peninsula.

Sample	Site	Common Name	Latin Name	Portion	Δ^{13}C	Δ^{15}N
Aquatic Fauna						
DH176	Copacabana	carachi amarillo	*Orestias* sp.	meat	−16.6	5.2
DH186	Copacabana	ispi	*Orestias* sp.	meat	−22.4	−
DH187	Copacabana	carachi negro	*Orestias* sp.	meat	−20.3	−
DH188	Copacabana	catfish	*Astroblepus* sp.	meat	−15.6	7.1
DH190	Copacabana	frog	*Telmatobius* sp.	meat	−17.7	8.6
DH386	Copacabana	such'l	*Trichomycterus* sp.	meat	−13.4	6.5
Terrestrial Fauna						
DH182	Cusijata	alpaca	*Lama pacos*	meat	−23.1	6.0
DH210	Copacabana	guinea pig	*Cavia porcellus*	meat	−25.4	7.4
DH387	Copacabana	chhuqa	*Fulicula gigantea*	leg meat	−15.8	6.1
DH388	Copacabana	chhuqa	*Fulicula gigantea*	breast meat	−17.4	5.5
Aquatic Flora						
DH383	Copacabana	t'utura or totora	*Scirpus* sp.	stem	−22.9	−
Terrestrial Flora						
DH384	Cochabamba	coca	*Erythroxylon coca*	dry leaves	−30.2	4.8
DH179	Copacabana	oca	*Oxalis tuberosum*	tuber	−26.4	1.8
DH180	Copacabana	chuño	*Solanum tuberosum*	tuber	−26.4	3.1
DH181	Copacabana	isañu	*Tropaeonlum tuberosum*	tuber	−26.9	−
DH178	Copacabana	maize	*Zea mays*	plant	−11.6	2.4
DH373	Copacabana	maize	*Zea mays*	popcorn	−11.4	4.8
DH374	Copacabana	maize	*Zea mays*	popped popcorn	−11.2	5.0
DH375	Copacabana	tawri or tarwi	*Lupinus mutabilis*	dry white legume grains	−23.8	−0.1
DH376	Copacabana	tawri or tarwi	*Lupinus mutabilis*	dry black legume grains	−26.4	0.1
DH377	Copacabana	tawri or tarwi	*Lupinus mutabilis*	dry black and white boiled legume grains	−26.6	0.6
DH378	Copacabana	kiwicha	*Amaranthus* sp.	dry amaranth grains	−12.0	5.8
DH379	Copacabana	quinua	*Chenopodium quinoa*	dry grains	−27.6	5.6
DH380	Copacabana	wild quinua	*Chenopodium* sp.	dry grains	−25.5	5.4
DH382	Copacabana	canihua	*Chenopodium pallidicaula*	dry grain	−25.0	6.0
DH385	Copacabana	llupt'a or llipt'a	*Chenopodium* sp.	burned quinoa stem	−22.7	−
DH381	Copacabana	wild sank'ayo or achacana		sundried native cactus	−12.1	−
DH389	Copacabana	wild sank'ayo or achacana		sundried native cactus	−11.7	−

algae follow this pattern of enrichment compared to their terrestrial counterparts, shown by the baseline fish samples here (Fig. 6) and by Miller et al. (2010).

Wild highland camelids tend to have more depleted carbon signatures, as compared with later domesticated camelids foddered on maize or marine algae (Finucane et al. 2006; Szpak et al., 2014). While PC foragers were likely hunting wild terrestrial mammals in addition to fishing, it is possible camelids did not feature regularly in diets, or were already being foddered with lake resources. The δ^{18}O values for PC individuals indicated a significantly wetter environment than during later periods (Figs. 9 and 10), which would have facilitated fishing and use of other protein-rich lake resources, such as lake birds and amphibians.

5.1.2. Early Horizon (EH)

During the EH, C$_4$ plants occasionally entered the diet, either through direct consumption by humans or human consumption of animals eating C$_4$ plants. The EH carbon apatite mean reflects values consistent with a 70:30 C$_3$:C$_4$ diet, with > 65% of protein coming from C$_3$ sources (Fig. 6) (Froehle et al., 2012). While C$_3$ resources still dominated the diet, there is clear inclusion of dietary C$_4$ in some form. People built agricultural terracing and expanded them dramatically during the EH, indicating an investment in new forms of food production (S.J. Chávez, 2018). It is possible that people grew maize or amaranths on these terraces and incorporated them into the increasingly horticultural subsistence plan. Alternatively, maize and amaranth could have been imported via newly emerging long-distance trade routes (Burger et al., 2000; Stanish et al., 2002). Archaeological and paleobotanical remains suggest that people across the lake basin increasingly relied on horticultural products overall, supporting these isotopic findings of some C$_4$ plant consumption (Bruno and Whitehead, 2003, Capriles et al., 2008, Capriles et al., 2014, Chávez & Thompson, 2006).

Occasional C$_4$ consumption during the EH may also reflect a religious use of C$_4$ plants, in connection with the newly emerged Yaya-Mama Religious Tradition. Logan et al. (2012) suggested that sharing maize beer (*chicha*) at temples on the Taraco Peninsula in the southern Titicaca Basin was central to ceremonies of ancestor veneration. Ethnographic studies note that wild quinoa is also locally used to make beer (S.J. Chávez, 2003). Those ceremonies likely worked to reinforce community bonds, through the sharing of that beverage (Janusek, 2008, Logan et al., 2012). The slight but notable amount of C$_4$ consumption during the EH may therefore be the result of sharing C$_4$-based beverages at temple events (although we cannot distinguish between liquid and solid C$_4$ consumption based on this evidence).

While there was a period of lake level decline during the EH (Abbott et al., 1997), it does not seem have affected fish consumption. EH nitrogen values reflect regular protein consumption, at slightly lower rates than during the Preceramic (Figs. 2, 5–7). Fish were likely the main source of this protein, based on recovery of fish bones and scales from Copacabana and southern lake basin sites (Capriles et al., 2008, Miller et al., 2010; Moore et al., 1999, Pearsall and deFrance, 2002) and evidence of net fishing from the southern lake basin (Moore, 2011). Terrestrial protein, in the form of guinea pigs and camelids, may also have been included in the diet. Faunal remains from southern lake basin sites show that while fish remains were dominant in the assemblage, camelid bones were also found in all contexts (Moore et al., 1999, Moore, 2011). Alongside the plant domestication and cultivation that occurred during the EH, it seems as though people were also occasionally using domesticated animals.

5.1.3. Early Intermediate Period (EIP)

Similar to the EH, individuals during the EIP consumed a mix of C$_3$ and C$_4$ resources (Figs. 5–7). It was during this period that more Yaya-Mama temples on the Copacabana Peninsula were constructed and/or expanded (S.J. Chávez, 2004a, 2012), perhaps underscoring the connection between ritual and C$_4$ resources. Notably, the least enriched oxygen isotope values came from the EIP, which may reflect boiling

Table 4
Mean isotope values by time period and sex. Indeterminate category includes indeterminate adults and juveniles. Groups with single individual excluded from sex averages but included in total averages. Starred averages are statistically significant outliers.

Period	Average δ^{15}N$_{co}$			Average δ^{13}C$_{ca-co}$			Average δ^{13}C$_{ap}$			Average δ^{13}C$_{co}$			Average δ^{18}O$_{ap}$			Total Average δ^{15}N$_{co}$	Total Average δ^{13}C$_{ca-co}$	Total Average δ^{13}C$_{ap}$	Total Average δ^{13}C$_{co}$	Total Average δ^{18}O$_{ap}$
	F	I	M	F	I	M	F	I	M	F	I	M	F	I	M					
PC	–	–	11.4	–	–	5.33	–	–	−11.82	–	–	−16.93	–	–	−9.78	11.54	5.26	−11.50	−16.64*	−9.81
EH	9.70	11.08	9.88	5.13	5.75	6.12	−13.39	−11.99	−12.68	−18.73	−17.75	−18.82	−10.03	−9.93	−10.30	10.37	5.73	−12.65	−18.32	−10.07
EIP	7.32	8.00	9.51	5.96	8.73	6.10	−12.72	−10.50	−12.62	−18.68	−19.23	−18.70	−10.06	−10.53	−10.44	8.77*	6.44	−12.34	−18.77*	−10.40
MH	9.93	10.35	–	7.03	5.44	–	−10.93	−13.06	–	−17.90	−18.5	–	−10.60	−10.21	–	10.24	5.87	−12.48	−18.34	−10.32
LIP	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9.67	4.27*	−14.63*	−18.9	−10.27
COL	–	–	12.25	–	–	7.05	–	–	−12.10	–	–	−19.15	–	–	−10.40	12.1	7.27*	−11.9	−19.17	−10.33
Total Mean	8.98	9.81	10.76	6.04	6.64	6.15	−12.35	11.85	−12.31	−18.34	−18.49	−18.4	−10.10	−10.22	−10.23	10.45	5.81	−12.58	−18.36	−10.20

(PC = Preceramic, EH = Early Horizon, EIP = Early Intermediate Period, MH = Middle Horizon, LIP = Late Intermediate Period, COL = Colonial).

water – a necessary step in preparing *chicha*. While it is difficult to say that the combination of isotope values reflects *chicha* consumption (Gagnon and Juengst 2019), it is an interesting possibility.

Nitrogen values are significantly less enriched in ^{15}N during the EIP, and spacing between EIP carbon apatite and collagen values suggests a decrease in fish consumption (Figs. 2 and 5). Given the proximity of all sites on the Copacabana Peninsula to the lake, this is somewhat surprising – fish should have been easily accessible. This pattern of decreased fish consumption correlates with evidence from two sites in the southern lake basin, through isotopic analyses at Lukurmata (Berryman, 2010:214) and analysis of fish remains from Taraco Peninsula sites (Capriles et al., 2008; Moore, 2011).

Fish remains decreased in number (based on NISP, weight, and density) and size during the EIP at Kala Uyuni and other Taraco Peninsula sites (Capriles et al., 2008; Moore, 2011). In contrast, there was an increase in bird bones and domesticated plant diversity (Bruno and Whitehead, 2003, Capriles et al., 2008, Capriles et al., 2014). Capriles et al. (2008) suggested "(t)he sharp decline in fish consumption and discard was a possible consequence of several factors including a greater variability in the water regime (Abbott et al., 1997), an increasing human population pressure (Bandy, 2004), and the possible depletion of wild resources" (Capriles et al., 2008:124).

Oxygen isotopes reported here are somewhat unclear regarding environmental change and its impact on diet. The most depleted oxygen values came from EIP individuals, but the mean and median were not statistically significantly lower than all other periods (Figs. 9 and 10). In fact, EIP individuals showed the widest range of oxygen values of all samples. Oxygen isotopes can reflect local environmental conditions, movement of individuals between different water sources, and/or storage and preparation of water. Baseline δ^{18}O$_{mw(VSMOW)}$ values collected from Lake Titicaca surface water in 2001 and 2002 ranged from − 12.6‰ to − 17.6‰ (Knudson, 2009). When converted from δ^{18}O$_{ap(VPDB)}$ to δ^{18}O$_{mw(VSMOW)}$ values (as described in the isotope background section), the δ^{18}O$_{ap}$ values reported here are mostly in the upper end of that range, suggesting that the lake was an important, but not the sole, water source in the past. The averaged values from our human samples cannot unfortunately address seasonal fluctuations in lake levels or precipitation.

Despite this limitation, the variety of EIP values may reflect diverse water source use, or responses to fluctuating environmental conditions, or both. Based on lake cores, we know there were significant fluctuations in lake levels during the EH, the EIP, and the LIP. The first decline in lake levels, occurring around 400 BCE, may have been as much as 12–15 m below previous levels (Abbott et al., 1997) but does not seem to have greatly impacted diet, as reflected by isotopes. However, the second decline occurred 500 years later, around CE 100 and lake levels were not restored until CE 350. This coincides with the first half of the EIP, and the decrease in protein consumption documented by the isotope results presented here. Thus, it seems likely that the wide range of oxygen isotope values identified during the EIP reflects use of a variety of water sources, coinciding with the fluctuating environmental conditions during this time.

While consumption of special beverages during Yaya-Mama ritual may have slightly increased C$_4$ resource use, it seems environmental trends changed access to resources and strongly impacted subsistence choices. Both ritual significance and environmental constraints are, of course, not mutually exclusive in driving resource use – the functional availability and ritual significance of resources could have been intertwined for EH and EIP communities as they made choices about what types of foods to prioritize. However, importantly, what these data demonstrate is that the documented lake level changes correlated with isotopic shifts in diet, and the emergence of new subsistence strategies.

5.1.4. Middle Horizon (MH)

The C$_4$ and protein consumption patterns shifted again in the MH, when Tiwanaku, the first regional state, exerted influence over the lake

Table 5

Results for 66 sampled individuals from the Copacabana Peninsula. Sample number refers to the number assigned to that sample during collection in Bolivia. Samples collected by Sara Juengst are denoted by sj, samples collected by Dale Hutchinson are denoted by dh. # indicates outlier dietary isotope values. * indicates outlier oxygen values. Cells with dashes indicate that data is not available.

Sample No.*	Site	Provenience	Period	Ind. #	Sex	Age cat	Sample type	wt %N	wt %C	%coll yield	C:N	$\delta^{15}N_{co}$	$\delta^{13}C_{ca\text{-}co}$	$\delta^{13}C_{ap}$	$\delta^{13}C_{co}$	$\delta^{18}O_{ap}$
sj18	Muruqullu	Tumba 10	PC	4	PM	Adult	tibia	14.3	39.8	7.3	3.2	11.3	6.2	−11.5	−17.7	−9.6
sj21	Muruqullu	Tumba 11	PC	1A	M	Young Adult	fibula	14.5	40.1	8.5	3.2	10.9	5.9	−11.9	−17.9	−9.6
sj28	Muruqullu	Tumba 10	PC	2	M	Adult	rib	14.7	40.8	8.5	3.2	12	4.2	−10.9	−15.2	−9.6
sj27	Muruqullu	Tumba 9	PC	4	M	Adult	rib	15.0	41.5	15.5	3.2	11.4	5	−12	−16.9	−10.1
dh124#	Kusijata	Tumba 3	PC	1	M	Adult	femur	–	–		–	–	–	−12.8	–	−10.0
sj31	Muruqullu	Tumba 9	PC	2	I	Juvenile	tibia	14.7	40.5	7.3	3.2	12.1	5	−10.5	−15.5	−9.1
dh125	Kusijata	Tumba 4	PC	1	F	Adult	femur	–	–		–	–	–	−10.9	–	−10.7
sj33	Muruqullu	Tumba 38	EH	3	F	Adult	humerus	–	–	0.6	–	–	–	−13.4	–	−10.2
sj30*	Muruqullu	Tumba 39	EH	1	I	Juvenile	humerus	15.3	42.0	17.8	3.2	12.8	4.4	−13.8	−18.2	−8.8
sj14	Muruqullu	Tumba 37	EH	1	I	Juvenile	radius	15.0	41.3	13.6	3.2	13.8	3.2	−8.9	−12.1	−9.0
sj16	Muruqullu	Tumba 40	EH	1	I	Juvenile	tibia	13.1	36.1	N/A	3.2	9.2	7.6	−11.2	−18.8	−9.6
sj20	Muruqullu	Tumba 22	EH	2	I	Young Adult	radius	14.7	40.4	8.1	3.2	11.2	6.8	−11.6	−18.5	−10.1
sj23	Muruqullu	Tumba 38	EH	1	I	Juvenile	fibula	14.5	39.6	7.0	3.2	8.8	6.8	−12.5	−19.2	−10.2
sj24	Muruqullu	Tumba 23	EH	1	I	Adult	radius	14.0	39.0	3.8	3.2	10.7	4.6	−13.6	−18.2	−10.4
sj29	Muruqullu	Tumba 22	EH	3	I	Adolescent	humerus	11.5	31.7	2.2	3.2	11.2	5	−13.1	−18.2	−10.5
sj42	Muruqullu Pata	Tumba 1, Trinchera Norte	EH	1	I	Adult	long bone	13.8	38.5	4.8	3.3	10.9	7.6	−11.2	−18.8	−10.8
sj25#	Muruqullu	Tumba 41	EH	1	M	Young Adult	fibula	14.7	40.4	6.5	3.2	10.3	7.2	−11.2	−18.4	−10.2
sj26	Muruqullu	Tumba 38	EH	2	PF	Adult	humerus	–	–	1.2	–	–	–	−13	–	−10.4
sj17	Muruqullu	Tumba 31, P5	EH	3	PF	Young Adult	humerus	11.3	31.6	1.2	3.3	11.5	5	−13	−18	−10.5
sj34	Muruqullu	Tumba 29	EH	2	PF	Young Adult	femur	–	–	0.9	–	–	–	−12.9	–	−10.5
sj32	Muruqullu	Tumba 22	EH	1	PF	Adult	humerus	14.4	39.8	6.7	3.2	10.4	5.3	−13.8	−19.1	−10.7
sj5	Cundisa	Tumba 92	EH	1	PM	Adult	femur	14.7	40.5	10.9	3.2	9.7	6	−12.7	−18.8	−9.9
sj22	Muruqullu	Tumba 29	EH	1	PM	Adult	humerus	12.8	35.6	1.9	3.2	10.3	5.8	−13	−18.8	−10.1
sj15#	Muruqullu	Tumba 29	EH	5	PM	Young Adult	femur	14.0	38.7	3.4	3.2	11	3.9	−14.3	−18.2	−10.3
sj19	Muruqullu	Tumba 31, P5	EH	1	PM	Adult	humerus	14.2	38.9	4.1	3.2	8.9	7.1	−12.3	−19.4	−10.6
sj35	Huayllani	Rasgo 1	EH	1	PM	Young Adult	fibula	14.8	40.6	7.0	3.2	9.1	6.7	−12.6	−19.3	−10.7
dh127*	Cundisa	Tumba 11(125)	EH	1	F	Adult	tibia	–	–		3.5	8.5	4.8	−13.9	−18.7	−8.1
dh206	Cundisa	Tumba 10(124)	EH	1	F	Adult	rib	–	–		3.3	8.4	5.4	−13.7	−19.1	−9.8
dh191	Ch`isi	40A-28D Nivel 2	EIP	1	F	Adult	rib	–	–		3.3	7.3	6.3	−12	−18.3	−9.9
dh194	Ch`isi	4D-3C Tumba 1	EIP	1	F	Adult	rib	–	–		3.3	7.3	7.2	−11.2	−18.4	−11.1
dh197#	Ch`isi	87C-88B	EIP	2	F	Adult	femur	–	–		3.3	7	4.7	−14.1	−18.8	−9.6
dh199	Ch`isi	30B	EIP	1	F	Adult	femur	–	–		3.3	6.6	7	−11.6	−18.6	−9.4
dh208#	Ch`isi	16D, Nivels 4–7	EIP	1	F	Adult	rib	–	–		3.3	8.4	4.6	−14.7	−19.3	−10.3
sj41	Tawa Qeñani	Tumba 1	EIP	1	I	Juvenile	tibia	14.3	39.6	5.6	3.2	9.6	9.3	−10.2	−19.5	−10.0
sj40	Tawa Qeñani	Tumba 1, Pozo 5, Nivel 2	EIP	1	I	Juvenile	rib	15.2	41.7	12.9	3.2	7.9	8.1	−10.7	−18.8	−10.7
dh200	Ch`isi	55B-C Nivel 1	EIP	1	I	Adult	femur	–	–		3.3	6.5	8.8	−10.6	−19.4	−10.9
dh192	Ch`isi	87C-88B	EIP	1	M	Adult	rib	–	–		3.3	7.8	4.8	−14.3	−19	−10.5
dh193	Ch`isi	35B-34C	EIP	1	M	Adult	rib	–	–		3.3	7.6	6.5	−11.7	−18.2	−11.7
dh195#	Ch`isi	3C-4D Tumba 2	EIP	1	M	Adult	rib	–	–		3.3	9.5	5.3	−11.5	−16.8	−11.1
dh196	Ch`isi	10A-B	EIP	1	M	Adult	rib	–	–		3.3	8.4	4.6	−13.7	−18.3	−10.0
dh198*	Ch`isi	32B	EIP	1	M	Adult	rib	–	–		3.3	7.9	6.3	−12.5	−18.7	−9.0
dh201	Ch`isi	26 AB	EIP	1	M	Adult	rib	–	–		3.3	8.7	6.2	−12.8	−19	−10.9
dh204	Cundisa	Tumba 8(122)	EIP	1	M	Adult	rib	–	–		3.3	9	4.8	−13.8	−18.6	−10.4
dh205	Cundisa	Tumba 8(122)	EIP	2	M	Adult	rib	–	–		3.3	8.4	6.2	−12.5	−18.7	−9.8
sj10#	Cundisa	Tumba 29	EIP	3	PM	Adolescent	rib	15.0	41.2	13.9	3.2	10.7	6.7	−13	−19.7	−10.8
sj7	Cundisa	Tumba 88	EIP	1	PM	Young Adult	fibula	14.9	41.1	10.5	3.2	11.6	6.6	−12.2	−18.8	−11.2
sj4	Cundisa	Tumba 114	EIP	1	PM	Adolescent	rib	15.0	41.4	15.1	3.2	11.4	6.9	−12.1	−18.9	−9.7
sj2	Cundisa	Tumba 29	EIP	2	PM	Adult	humerus	14.6	40.0	6.9	3.2	11	7.5	−12.1	−19.6	−11.1
sj6	Cundisa	Tumba 88	EIP	2	PM	Adult	humerus	15.1	41.4	11.0	3.2	11.6	6.9	−11.9	−18.8	−11.4
sj38	Qopakati	Pozo N26.5 W25.6	MH	1	I	Juvenile	rib	14.9	40.7	12.5	3.2	9.3	6.4	−13.3	−19.7	−10.2
sj39#	Qopakati	Pozo N23W26, Ext SE Corner	MH	1	PF	Adult	long bone	14.1	39.5	4.9	3.3	11.3	8.1	−11.5	−19.5	−11.1
dh202	Qhot'a Pata	1A Nivel 4	MH	1	F	Adult	rib	–	–		3.3	9	6.8	−11.8	−18.6	−10.2
sj13	Cundisa	Tumba 109	MH	1	I	Juvenile	femur	14.5	39.8	19.1	3.2	11.1	4.9	−12.2	−17.1	−9.7
sj12	Cundisa	Tumba 25	MH	1	I	Juvenile	fibula	15.3	41.9	14.0	3.2	11.2	4.8	−13.3	−18.1	−10.0

Table 5 (*continued*)

Sample No.*	Site	Provenience	Period	Ind. #	Sex	Age cat	Sample type	wt %N	wt %C	%coll yield	C:N	$\delta^{15}N_{co}$	$\delta^{13}C_{ca-co}$	$\delta^{13}C_{ap}$	$\delta^{13}C_{co}$	$\delta^{18}O_{ap}$
sj8	Cundisa	Tumba 19	MH	1	I	Adult	fibula	15.1	42.1	13.1	3.2	10.3	4.6	−14.1	−18.7	−10.1
sj9	Cundisa	Tumba 25	MH	2	I	Juvenile	humerus	15.2	42.0	14.7	3.2	10.6	5.4	−12.8	−18.2	−10.1
sj1	Cundisa	Tumba 20	MH	1	I	Adolescent	radius	14.6	40.4	8.3	3.2	9.2	6.5	−12.2	−18.7	−10.9
sj11	Cundisa	Tumba 84	MH	1	I	Adult	fibula	14.9	41.0	14.6	3.2	10.5	5	−13.5	−18.5	−10.9
sj3#	Cundisa	Tumba 64	MH	2	PF	Adult	humerus	14.9	40.0	11.6	3.2	9.5	6.2	−9.5	−15.6	−10.5
dh126	Cundisa	Tumba 2(116)	MH	1	I	Adult	rib	–	–	–	3.5	10.62	5.9	−13.1	−19	−9.8
dh177	Ch'isi	TC 7	LIP	1	F	Adult	rib	–	–	–	3.3	9.2	4.7	−14.3	−19	−10.4
dh184	Ch'isi	TC 5	LIP	1	I	Adult	rib	–	–	–	3.3	9.7	4.4	−14.8	−19.2	−9.6
dh183	Ch'isi	TC 6	LIP	1	M	Adult	rib	–	–	–	3.3	10.1	3.7	−14.8	−18.5	−10.8
sj36	Mallku Pukara	Pozo 16S18S, Ext W, Tumba 1	COL	1	M	Adult	femur	14.0	39.2	4.9	3.3	13.2	8	−11	−19	−10.0
sj43	Mallku Pukara	Pozo 12.5, Nivel 1, Tumba 1	COL	1	PF	Adult	rib	14.6	40.4	12.1	3.2	11.8	7.7	−11.5	−19.2	−10.2
sj37	Mallku Pukara	Tumba 2	COL	1	PM	Young Adult	rib	15.3	42.3	17.1	3.2	11.3	6.1	−13.2	−19.3	−10.8

(PC = Preceramic, EH = Early Horizon, EIP = Early Intermediate Period, MH = Middle Horizon, LIP = Late Intermediate Period, COL = Colonial).

basin and beyond. While Yaya-Mama ceremonies may have involved *chicha* (Logan et al., 2012), it is clear that Tiwanaku ceremonies centered on it. There is abundant ceramic, archaeobotanical, and isotopic evidence of maize consumption during the MH at sites in the southern lake basin, the *altiplano,* and at lower-altitude sites in Cochabamba and the Moquegua Valley, Peru (Berryman, 2010, Goldstein, 2003, Goldstein et al., 2009, Janusek, 2008, Somerville et al., 2015). Whether or not the C4 signatures represent consumption of liquid maize is unclear.

For this study, it is notable that overall C4 resource consumption drops on the Copacabana Peninsula during the MH, shown by more negative carbon apatite and collagen values and closer carbon apatite-collagen spacing (Figs. 4–6, 8). Additionally, oxygen values are slightly less negative, suggesting either more precipitation, different water sources, or less reliance on stored and boiled water (Figs. 9 and 10). Instead of a reliance on C4 resources or clear evidence of direct C4 consumption, we see a return to lake resources.

This is a surprising finding for the MH, given the ritual and dietary focus on maize at other Tiwanaku sites, which may well be exemplified by the archaeological deposits of maize in nearly all cultural contexts at Tiwanaku during the MH (Hastorf et al., 2006). Perhaps the extreme proximity of the Copacabana sites to the lake (i.e., all within 100 m of the lakeshore) and the water level recovery after the drought (Abbott et al., 1997) made lake resources more appealing to Copacabana Tiwanaku groups, as opposed to maize consumption. This pattern of low lakeside C4 consumption vs high C4 consumption at Tiwanaku itself may also reflect a larger trend in Tiwanaku social organization: labor specialization. Many Tiwanaku communities were oriented around specialized labor activities (Becker, 2017, Janusek, 2008). Perhaps the focus on fish consumption for Copacabana peoples indicates specialized fishing communities.

Alternatively, local citizens may have maintained ties to Tiwanaku for religious, political, and/or economic reasons (shown by Tiwanaku keros and ceramics found in MH tombs) but also developed their own local identities and practices (demonstrated by miniature, unfired ceramic objects also found in these tombs) (S.R. Chávez, 2018). Further analysis of Tiwanaku settlements (yet to be identified on the Copacabana Peninsula) and mortuary goods (S.R. Chávez, 2018) may help clarify why, based on isotopic data, these Tiwanaku-affiliated individuals were not consuming C4 resources like their fellow Tiwanaku citizens.

5.1.5. Late Intermediate Period (LIP)

The trend of decreased C4 consumption continues into the LIP, with some of the least positive carbon values in the whole sample. In particular, LIP carbon apatite values (reflecting total diet) are statistical outliers based on ANOVA testing (F (5, 60) = 3.186, p = .013), with the group mean significantly more negative than other periods (Fig. 8). This group mean is the only one to fall between centroids 1 and 4 when compared to Froehle et al. (2012) (Fig. 6), indicating these individuals included proportionally more C3 resources in their diet compared to people during other periods. It is important to note that the LIP sample only includes three individuals; however, the values for all isotopes are tight and there are no outlier values.

The LIP is generally considered a time of regional disintegration, as Tiwanaku lost influence in the lake basin. Based on LIP site fortifications and evidence of skeletal trauma, it seems clear that raids were regularly a concern for lake basin denizens during this time (Arkush, 2008, 2011, Bandy, 2001, De la Vega et al., 2005, Juengst et al., 2017b, Langlie, 2018) (although see Zovar, 2012 for analysis of an unfortified LIP lake basin site).

Given this volatile landscape, terraced farming may have been a riskier undertaking, compared with fishing or herding. Langlie (2018) suggested that in the northern lake basin, LIP peoples dealt with this risk by using a mixed strategy of herding and small scale farming. The isotope values reported here are partially consistent with this pattern: demonstrating less investment in terraced farming through depletion of

C_4 resource consumption. However, the three LIP individuals' nitrogen isotope signatures are only slightly higher than those of camelids (Fig. 2; Table 3) (Finucane et al., 2006). If these individuals were regularly consuming camelids, we would expect their nitrogen values to be a trophic level (2-5‰) higher. The average carbon apatite and collagen spacing ($\Delta^{13}C_{ca-co}$) is also quite narrow for this group (4.27‰) when compared to other periods (Table 3). This indicates a particular emphasis on C_3 and aquatic resources, rather than terrestrial protein. From this combination of isotopic values (depleted nitrogen and narrow carbon apatite and collagen spacing), it seems unlikely that LIP peoples were consuming camelids regularly.

Notably, lake levels were low during the LIP (Cross et al., 2000), which may have limited access to fish and further depleted nitrogen values for LIP individuals. Perhaps during the LIP, Titicaca Basin peoples practiced smaller scale farming of C_3 plants and collecting wild lake plants, rather than fishing or herding. However, a larger sample size is needed to test and clarify these trends.

5.1.6. Colonial Period (COL)

Isotope signatures from COL individuals reflect a move away from lacustrine resources and towards terrestrial protein, based on the statistically significant wide carbon spacing and high nitrogen values (Figs. 2, 5; Table 3–5). These three individuals have not been directly dated but were buried in very shallow stratigraphic layers with no associated artifacts. They likely lived in the Early Colonial Period, when Copacabana was a well-established Spanish pilgrimage center (MacCormack, 1984, 2010; Christie, 2019) and local economic production focused on a mix of Spanish *hacienda* and locally owned *ayllu* based farming (Klein, 1993). While people still raised native crops and animals, Spanish-introduced sheep had become a central part of the agricultural regime (Klein, 1993). The wide carbon spacing and high nitrogen values of the Colonial sample may thus represent the inclusion of sheep, or sheep by-products such as cheese, in daily diets. The Colonial sample only includes three individuals from undated contexts; a more secure sample is needed to clarify these ideas. However, as with the LIP, the values are tight for all isotopes and there are no outlier values.

5.2. Individual outliers and strontium

Certain individuals showed stable dietary isotope ratios that deviated from the rest of the population (see Table 5). These outliers did not share time periods, demographic categories, nor other mortuary traits (i.e., burial goods, style or location) that would identify them as different from the rest of their group. Instead, these outlying individuals may have been eating different foods because they were regularly traveling to other parts of the Andes, increasing their access to novel foods.

A previous strontium study of burials from the Copacabana Peninsula identified some non-local individuals (Juengst, 2017). Importantly, every dietary outlier identified here was also identified as non-local or semi-local in that previous study (with the exception of two individuals [MQT41 and MQT29] from the site Muruqullu, as they were not included in the earlier strontium study). Strontium isotopes from dental enamel are markers of local geology during childhood; individuals with signatures different from local baselines are interpreted as migrants or regular travelers through other regions (Knudson, 2008).

The strontium study recorded long-distance mobility early in life, based on non-local strontium signatures in dental enamel (Juengst, 2017). The dietary isotopes reported here reflect consumption closer to the time of death, as bone continually renews over the life course (Parfitt, 1983). It is thus possible the outlier results presented here provide evidence for on-going mobility in adulthood for these individuals. The individuals who lived elsewhere as children may have continued to move between the lake basin and those other areas, and thus consumed different resources than their locally born counterparts. It is also possible that these individuals were integral to trade networks

active during the EH and EIP, and helped bring new foods into the region (Burger et al., 2000, Juengst, 2017).

Several juvenile individuals (MQT9IN2, MQT37IN1, MQT39IN1) also had $\delta^{15}N$ values enriched in ^{15}N. We suggest two possible explanations for juvenile dietary outliers: they may have been breastfeeding (as they were aged 2–5 years) (Fuller et al., 2006, Schurr, 2018, Wright and Schwarz, 1998), or extremely stressed individuals who began to self-catabolize prior to death (Fuller et al., 2005). The most ^{15}N-enriched sample in this study came from MQT37IN1, an EH juvenile estimated to be between six and eight years old at the time of death. While it is unlikely that this individual was still breastfeeding at its estimated age of death, this individual also had healed periosteal reactions of their tibiae, suggesting that they had previously survived stress episodes. Perhaps their high nitrogen signature reflects on-going stress, which ultimately resulted in their death. Previous studies show that skeletal evidence for disease increased overall during the EH and EIP (Juengst, 2018, Juengst et al., 2017c); some of the young individuals in our study that exhibit high ^{15}N enrichment are therefore likely connected to stress episodes rather than high levels of meat consumption.

5.3. Overall trends

Throughout all periods, the results presented here show a generally mixed diet of plants and animals with limited C_4 contributions (Figs. 2–7). Diet and sex were not significantly correlated during any periods. Only the Preceramic and LIP populations had significantly different carbon collagen and carbon apatite values, respectively; and even considering these deviations, people did not include nor entirely exclude significant amounts of C_4 resources. The most meat consumption occurred in the earliest and most recent periods, the Preceramic and Colonial. These samples were small but had higher nitrogen values than all other samples.

In the Andes, C_4 isotopic signatures are usually interpreted as representing maize consumption; however, as Cadwallader et al. (2012) and Turner et al. (2018) remind us, amaranths may also contribute a C_4 signature to the diet. On the Copacabana Peninsula, it seems probable that any dietary inclusion of C_4 at least partially reflects maize because of associated cultural and botanical evidence for maize production, processing, and consumption (S.J. Chávez, 2018; Chávez and Thompson 2006; Logan et al. 2012; Whitehead, 1999:97); although evidence of amaranth consumption has been recovered from the region as well (Lee, 1997, Pearsall and deFrance, 2002; Whitehead, 1999:97).

Lacustrine plants and fish may also be playing a role in more positive carbon collagen and carbon apatite signatures as many Titicaca aquatic plants are enriched in ^{13}C and have very high $\delta^{13}C$ signatures (Miller et al, 2010). While we have not documented these aquatic plants archaeologically (possibly due to issues of preservation), wetland-reliant sedges have been identified from archaeological contexts on the neighboring Taraco Peninsula (Bruno and Hastorf, 2016). It is thus possible that some waterweeds and algae were included in the local diet of humans and/or their camelids.

6. Conclusions

Diets shift for many reasons, including availability of local resources, introduction of new products, new trade networks, and the social value of food items. Here, we investigated how and why dietary patterns changed (or remained the same) on the Copacabana Peninsula over several thousand years. The Early Horizon and the Early Intermediate Period, and particularly the transition between them, were important times during Andean prehistory, as during this time, people built complex social and political networks across the region, laying the foundation for state development during the Middle Horizon (S.J. Chávez, 2004a, 2018).

Understanding how subsistence strategies and trade networks were functioning during this time, and how new foods entered and circulated

in this network, is important therefore to our understanding of the Tiwanaku polity, and Andean societies more broadly. In particular, we note that while times of drought generally corresponded with dietary changes, groups adopted different strategies to cope with environmental shifts over time. Additionally, we demonstrate the heterogeneity of diet within the Tiwanaku state, as Copacabana denizens ate significantly different diets than Tiwanaku site dwellers. Instead of a unilineal movement away from fished and foraged resources towards agriculture, Copacabana peoples used a variety of subsistence strategies and resources over time, in response to local environmental and social changes.

CRediT authorship contribution statement

Sara L. Juengst: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing - original draft, Writing - review & editing. **Dale L. Hutchinson:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Methodology, Supervision, Validation, Visualization, Writing - original draft, Writing - review & editing. **Karen Mohr Chávez:** Funding acquisition, Project administration, Resources, Supervision. **Sergio J. Chávez:** Funding acquisition, Project administration, Resources, Supervision, Writing - review & editing. **Stanislava R. Chávez:** Project administration, Writing - review & editing. **John Krigbaum:** Methodology, Resources, Writing - review & editing. **Theresa Schober:** Methodology, Resources. **Lynette Norr:** Methodology, Resources.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability statement

Please contact first author to access data.

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