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Human Ecology of Shellfish Exploitation at a Prehistoric Fishing-Farming Village on the Pacific Coast of Mexico

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ABSTRACT

Shellfish remains excavated from an early agricultural village on the Pacific Coast of Mexico (Guerrero) indicate a dietary shift from locally obtained estuarine shellfish (1400–1100 BC) to a greater diversity of mollusks collected from more distant marine environments (900–500 BC). The timing of this shift suggests that it occurred as human populations increased and impacted the availability of local estuarine resources. We argue that this prompted the incorporation of a more diverse array of shellfish species harvested at greater distances or obtained via trade, possibly with the use of boats to transport shellfish and other resources back to the village.

Keywords behavioral ecology, formative period, historical ecology, maritime adaptations, Mesoamerica, mollusks, optimal foraging theory

INTRODUCTION

Ancient shell middens along the coasts of the world's oceans indicate the importance of shellfish exploitation for anatomically modern humans as they expanded out of Africa over 100,000 years ago (Erlandson 2001). Most shellfish are sessile, distributed in aggregated clumps, and available year round. Little or no specialized technology is

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required to collect mollusks and people of all ages (men and women, young and old) can collect them easily (Bird et al. 2002; Erlandson 1988; Glassow and Wilcoxon 1988; Rick and Erlandson 2009; Yesner 1980). Because of these characteristics, shellfish are a convenient and plentiful source of protein and often a dietary staple in coastal environments. During the Holocene shellfish and other marine resources provided a stable subsistence base for growing populations and the emergence of complex hunter-gatherer societies in some regions (e.g., California, Kennett 2005; Rick et al. 2005; Northwest Coast, Ames and Maschner 1999). People living in areas of high productivity like coastal and estuarine regions were often slower to implement and commit to agriculture as they had access to a wide variety of aquatic prey such as shellfish and fish (Piperno 2006).

The characteristics that make shellfish an attractive economic resource also make them particularly susceptible to predation (Erlandson and Rick 2008). The differential impacts of human predation on shellfish species depend on species' habitats, geographic distribution, available refugia, and life history characteristics as well as human preference for particular species and technologies used (Claassen 1986; Erlandson et al. 2011; Mannino and Thomas 2002; Thacker 2011). Heavy predation and long-term human selection of individuals can cause population structures to change so that the average size of available individuals in an area decreases over time along with alterations in species composition (Braje et al. 2007; Erlandson et al. 2011; Mannino and Thomas 2002; Milner et al. 2007; Rick and Erlandson 2009). Because of the ease of procurement, clumped shellfish that are found in shell-beds (like oysters and mussels) or those found on the surface (gastropods, oysters, mussels) would be more prone to population decline due to predation compared to shellfish with more elusive behavioral attributes (e.g., burrowing taxa; de Boer et al. 2000). Larger bodied solitary species are also prone to decline in number. An increase in diversity in species preyed upon, changes in age and size profiles, as well as shifts to focus on alternative shellfish species through time can signify human-caused resource depression sometimes influenced by natural processes (de Boer et al. 2000; Erlandson and Rick 2008; Erlandson et al. 2004; Klein et al. 2004; Mannino and Thomas 2002).

Here we explore the effects of human predation on shellfish populations within the vicinity of the early agricultural village of La Zanja, located in the Acapulco Bay region of Guerrero, Mexico. Estuaries, sandy beaches, and rocky shorelines supported a remarkable diversity of molluskan species during the Middle and Late Holocene (Kennett et al. 2008). Shellfish populations have been strongly and negatively impacted during the last century with the expansion of Acapulco as a major urban center and tourist destination. Our study provides an environmental baseline for comparison with the contemporary distribution and diversity of shellfish taxa in this region of Mexico. This work also provides a glimpse at changing shellfish harvesting strategies as expanding agricultural populations impacted the more pristine coastal environments of Mexico. Using optimality models from behavioral ecology (optimal foraging theory [OFT]) we predict that resource depression at this settlement location would lead to expanding diet breadth and the acquisition of resources from more distant locations via long-range forays or trade. One of the unintended consequences of an increasing commitment to agriculture is population expansion and a host of associated environmental impacts (Hooke 2000) that effect the distribution and abundance of non-agricultural subsistence resources. The deposits at La Zanja span this critical interval of early agricultural commitment and expansion and we examine changing shellfish harvesting strategies within this context that are generally consistent with OFT predictions.

BACKGROUND

La Zanja is located 2 km from the Pacific Coast, south of Acapulco, at the confluence of the Sabana River and the Tres Palos Lagoon (see Figure 1). The site is located

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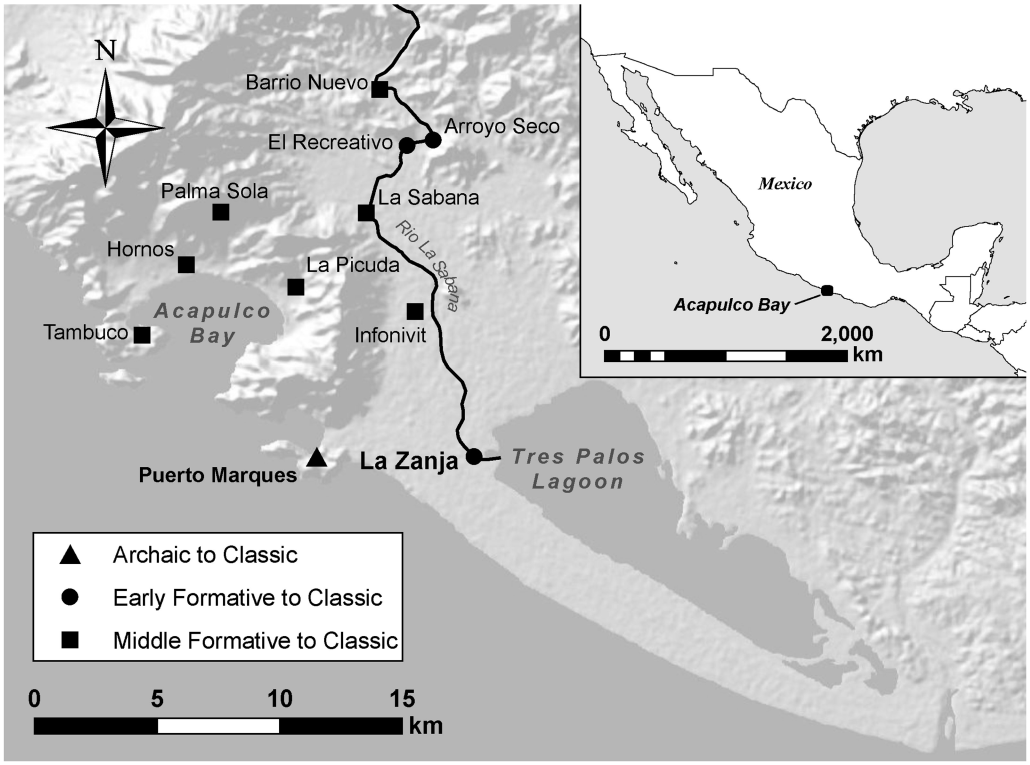

Figure 1. *Map of coastal Guerrero, Mexico showing the location of Las Zanja relative to other sites in the region.*

at the edge of the northeastern end of the estuary, on a narrow coastal plain (2.5–13 km wide) between the Sierra Madre del Sur and the Pacific Ocean. Stratified archaeological deposits in this low earthen mound site span the Early (∼1400–1100 BC) and Middle Formative (∼900–500 BC) periods of Mesoamerican prehistory (see below). The Formative Period (∼1800 BC–AD 300) followed a trajectory established during the Archaic Period (∼8000–1800 BC; Kennett 2012) of increasing reliance upon domesticated plants complemented by many wild foods (Flannery 1973, 1986; Kennett and Voorhies 1996; Kennett et al. 2006; Piperno 2006; Smith 2001; Voorhies 1996). Greater commitment to agricultural production required more intensive use of land surrounding central places, which altered habitats and gradually changed the relationship between human and local coastal and terrestrial environments (Doolittle 1990; Lentz 2000; Piperno 2006). New relationships were characterized by population growth, greater sedentism, environmental and social circumscription, and the emergence of social hierarchies that ultimately led to the first state institutions in Mesoamerica (Clark and Blake 1994; Kennett et al. 2006; Rosenswig 2009; Webster 2002).

Early excavations in the Acapulco region by Charles Brush between 1959 and 1960 identified a number of sites along the Sabana River and around Acapulco Bay (Brush 1969). Manzanilla López et al. (1991; Manzanilla López 2000) have greatly expanded Q3 our working knowledge of the prehistory in this region and reassessed the regional ceramic typology/chronology based on new excavations and Brush's original collections. Puerto Marqués is the earliest site in the region, dating to the Late Archaic (~3500 BC) and was occupied through the Classic Period (~AD 800; Brush 1969; Kennett et al. 2008; Manzanilla López 2000; Manzanilla López et al. 1991). Puerto Marqués is located directly on the coast and the faunal assemblage of this site is dominated by species from marine ecosystems in all periods. A deeply buried shell mound at Puerto Marqués was dated to the Late Archaic (3500–2000 BC); this mound shows the importance of coastal resources to early foragers in this area (Brush 1969; Kennett et al. 2008). La Zanja was established within a lagoonal/mangrove setting farther from the coast during the later part of the Early Formative (~1400 BC). The proximity of the two sites (~5 km) and the earlier founding of Puerto Marqués suggest that La Zanja was originally settled by a group of people from Puerto Marqués.

Laguna Tres Palos and the bay at Puerto Marqués were probably linked by a mangrove swamp during the early and middle Holocene but are now separated by a barrier beach (Kennett et al. 2004, 2008). Conditions in the modern lagoon change seasonally with the discharge of the La Sabana River and changing tidal influences as the inlet opens and closes to the Pacific Ocean (Kennett et al. 2004). The coastal lagoons and rivers provided access by watercraft to many areas along the coastline and seasonal inundation of the lower reaches of the coastal plain offered a form of natural irrigation that could have facilitated agriculture during the Formative Period. In this way La Zanja's location allowed for strategic use of a wide variety of resource patches with different prey within a 5-km radius of the site. The coastal plain and piedmont areas surrounding the site provided access to terrestrial mammals and the adjacent marine habitat supplied fish, shellfish, and sea turtles. A mangrove estuary along which the site is located offered additional local resources such as birds, lagoon fish, gastropods, and bivalves that required little time and effort to acquire. Aquatic invertebrates were also available from the intertidal mudflat near the site. A decrease in overall energetic returns from wild fauna over time at La Zanja probably coincided with a greater dependence on domestic plant foods, which would be complemented by protein from shellfish. Agriculture and high populations would have had a perceptible impact on local resources that may have necessitated forager-fisher-farmers to travel farther into different habitats to procure resources. Lagoon systems around the site could have provided efficient travel to more distant resource patches and the transport of these resources back to La Zanja via watercraft.

THEORETICAL FRAMEWORK

Human behavioral ecology (HBE) provides a set of models that researchers can use to explore complex ecological interactions within changing social and natural environments (Broughton and O'Connell 1999; Kaplan and Hill 1992; Kennett 2005; Kennett et al. 2009; Winterhalder and Kennett 2006; Winterhalder et al. 2010; Winterhalder and Smith 2000). Within the broader HBE framework, OFT provides models to evaluate and examine prehistoric subsistence strategies. Costs and benefits of different foraging behaviors are evaluated given a set of environmental parameters and the models assume that humans tend to make economically rational decisions that optimize energetic returns while minimizing investment costs and risk (Broughton and O'Connell 1999; Kaplan and Hill 1992; Smith 1983; Stephens and Krebs 1986). In OFT, benefits are estimated by caloric energetic returns of different prey items with costs including time spent in manufacturing tools, search, pursuit, and processing.

We use the prey and choice model and the Marginal Value Theorem here to explore shellfish harvesting strategies at La Zanja through the Early and Middle Formative Periods and the expansion of diet breadth at the through time. With long-term intensive use of a relatively homogenous local environment, usually associated with increasing populations and targeting of high-ranked species, the prey choice model predicts predation pressure that results in declining abundance of higher ranked large species (Broughton and O'Connell 1999; Kaplan and Hill 1992; Smith 1983). With resource depression, encounter rates with high-ranked foods decrease until foraging return rates decrease enough that foragers expand their diets to incorporate lower ranked prey items and the optimal diet becomes more diverse (Broughton and O'Connell 1999; Hawkes and O'Connell 1992; Kennett et al. 2006). The Marginal Value Theorem makes predictions about how long an individual will stay in a given resource patch before moving on to exploit another (Charnov 1976). Individuals will widen their foraging range as local food sources are impacted, and may focus on higher ranked prey to compensate for energy expended in travel until a diet that optimizes energetic returns is reached.

The prey choice model assumes homogeneity of prey distribution within the environment, but a division of the foraging area into resource patches allows application of measures of evenness and diversity within patches that are sensitive to resource depression and widening diet breadth (Nagaoka 2002). A decrease in encounter rates could prompt individuals to widen their search area or to target different patches. However, at a certain point, if high-ranked items become so depleted that the increase in search time is not met with sufficient returns, more low-ranked local resources may be added to increase diet breadth (Broughton and O'Connell 1999; Hawkes and O'Connell 1992; Hawkes et al. 1997). In this way, an increase in diversity indices can also signal a decrease in foraging returns. Hawkes and O'Connell (1992) point out that where the diet is relatively narrow, foragers will typically target high-ranked prey to justify costs, with high search times relative to handling time. They go on to say, "Conversely, where diet is broad and handling represents the bulk of foraging effort, improvements in handling efficiency would have large effects" (Hawkes and O'Connell 1992:64). As targeted prey species decline and high populations prevent the expansion of sedentary groups into less impacted environments, reliance on intensive food production with high handling costs may increase.

Within the La Zanja faunal assemblage, the highest ranked prey were marine turtles that were hunted locally while nesting on beaches and in the estuarine zone (Smith et al. 2007). Other high-ranked mammals found in the assemblage include deer and peccary; the energetic returns for these species may have been moderated by increased travel and search time in interior locations. Estuarine fish and shellfish may have individually represented a lower protein/energy contribution than larger animals, but were the easiest prey to acquire as they were present in abundance in the lagoon near the settlement. There is a tradeoff between energy capture and subsistence risk and the reliability of shellfish may have served the foraging goals of men, women, and children differently (Zeanah 2004). The habitats of marine fish and shellfish would require more time spent in travel to acquire than estuarine varieties, but were probably a more reliable and consistent food source than many of the larger animals. Madsen and Schmitt (1998) emphasize that prey items such as insects and shellfish can be collected in mass and that their dietary ranking is density dependent. They point out that when small animals are available in large amounts they become a high-ranked item and can displace larger prey in optimal diets. Many of the shellfish species in the La Zanja assemblage occur in clumps and were likely captured with mass harvesting techniques (e.g., rakes) and thus contributed to larger energetic returns compared with solitary animals of the same size.

METHODS

The La Zanja site is an earthen mound 3.2 m high with an area of 40,000 m^2. In 2001 we excavated a 2 × 2 m unit at the highest point in the mound down to a depth of 3.6 m in order to gain a complete view of Formative period occupation (20 cm levels; see Figure 2). Previous excavations at the site by Brush (1969), along with our own systematic auger tests, indicate that the Early and Middle Formative Period deposits are only represented in the center of the site. The

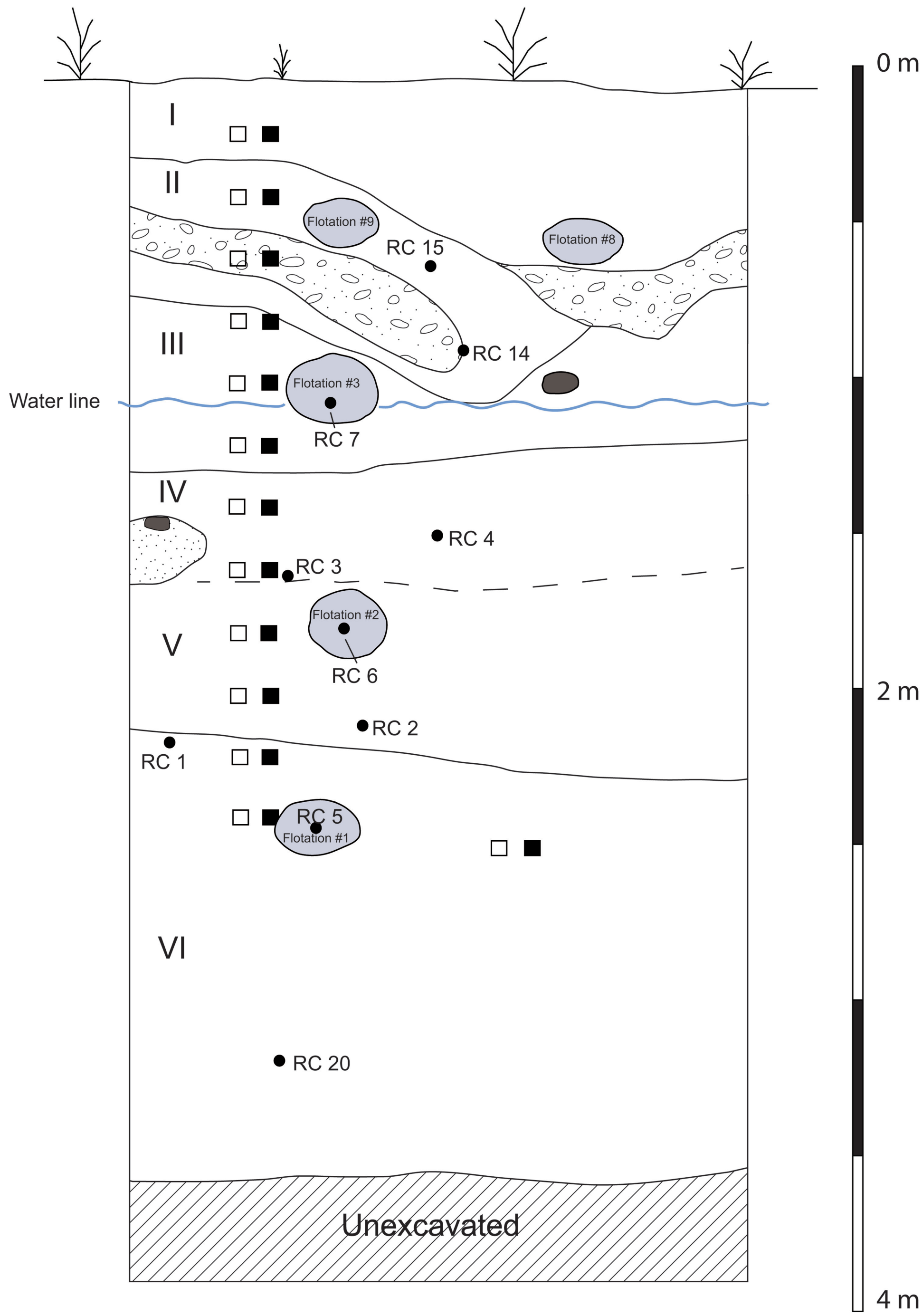

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Figure 2. *North profile of excavated unit at La Zanja showing Early and Middle Formative Period stratigraphic units and associated AMS ^{14}C dates (color figure available online).*

upper Middle Formative Period deposit extends more widely and is indicative of population expansion after the settlement was initially established in the Early Formative. The 2 × 2 m unit was placed in the center of the site to sample the stratigraphic superposition of Early and Middle Formative Period deposits. The study was exploratory due to budgetary constraints and additional work will be required to determine the degree of spatial heterogeneity of these deposits.

Pumps were used to excavate below the water table (~108 cm beneath the surface; Kennett et al. 2004). Stratigraphy was essentially horizontal and there were two major cultural components represented by unique artifact assemblages dating to the Early (360–240 cmbd) and Middle Formative (200–80 cmbd) Periods. Seven AMS ^{14}C dates were calibrated and modeled stratigraphically in OxCal 4.2 to establish the chronology for the site (Figure 3; Bronk Ramsey 2013; Kennett et al. 2011). Table 1 provides the 2-σ calibrated ranges for each date and the modeled age for each phase (or period). Dates were placed in an ordered sequence and modeled within two phases, Early and Middle Formative, based on stratigraphic association. The span of time represented by each dated event for the Early Formative phase is estimated to be between 24 and 344 years (~1400–1100 BC), with a total maximum duration for the phase of 846 years. The span of the dated events for the Middle Formative phase is between 53 and 354 years (~900–550 BC), with the total maximum duration estimated at 796 years. While the maximum duration of occupation at the site for the Early Formative is approximately 120 years longer than the Middle Formative, average durations for each phase (423 and 420 years, respectively) suggest comparable occupations of comparable duration. The Formative period occupation at La Zanja is contemporary with the growth of settlements on the Gulf Coast (San Lorenzo; Cyphers 1996; Cyphers et al. 2007–2008), Oaxaca (San Jose Mogote; Flannery and Marcus 2000), and the Soconusco (Paso de la Amada; Clark and Blake 1994).

Sediments from each 20-cm level of the unit were screened through 5-mm mesh with an additional 104-liter sample from each level passed through a 3-mm screen (Kennett et al. 2004). Shells in the assemblage were fragmented from processing, but large enough that the 5-mm sample considered here is representative. Field assessment of the 3-mm residue indicate that shellfish species smaller than 5 mm are rare in the assemblage. Levels analyzed are of equal volume (5.6 m^3) for both periods and the duration of occupation is similar so we argue that the samples are directly comparable. Poteate and Fitzpatrick (2013) have suggested that sampling less than 16% of zooarchaeological remains of a study population may produce results that are not statistically significant and are not representative. Though the assemblage analyzed represents a subsample of the greater population at the site, analysis of smaller units (e.g., 50 × 50 cm) are not uncommon for coastal settings. Shellfish are abundant in the excavation at La Zanja, and the overall zooarchaeological assemblage is closely mirrored by the diverse assemblage excavated at the nearby site of Puerto Márques. Previous research from both sites shows a trend of human predation that resulted in the reduced availability of high-ranked sea turtles from the Early to Middle Formative periods (Smith et al. 2007). Similar trends observed in the shellfish assemblage at La Zanja are likely to be representative of long-term changes in human foraging patterns that led to an increasing diet breadth. Modern trash was mixed into the upper 80 cm of the deposit and there was a single mixed level (200–220 cm) between the Early and Middle Formative Period components. These mixed deposits were excluded from our analysis.

Shellfish remains were identified using a comparative collection developed by Barbara Voorhies and Douglas Kennett (Table 2). We used the Number of Identified Specimens (NISP) and Minimum number of Individuals (MNI) to quantify taxonomic abundances for mollusk species. MNI and NISP are common zooarchaeological methods that are often highly correlated. MNI provides researchers with a close approximation of the number of individuals belonging to a study population (Classen 1998; Reitz and Wing 1999).

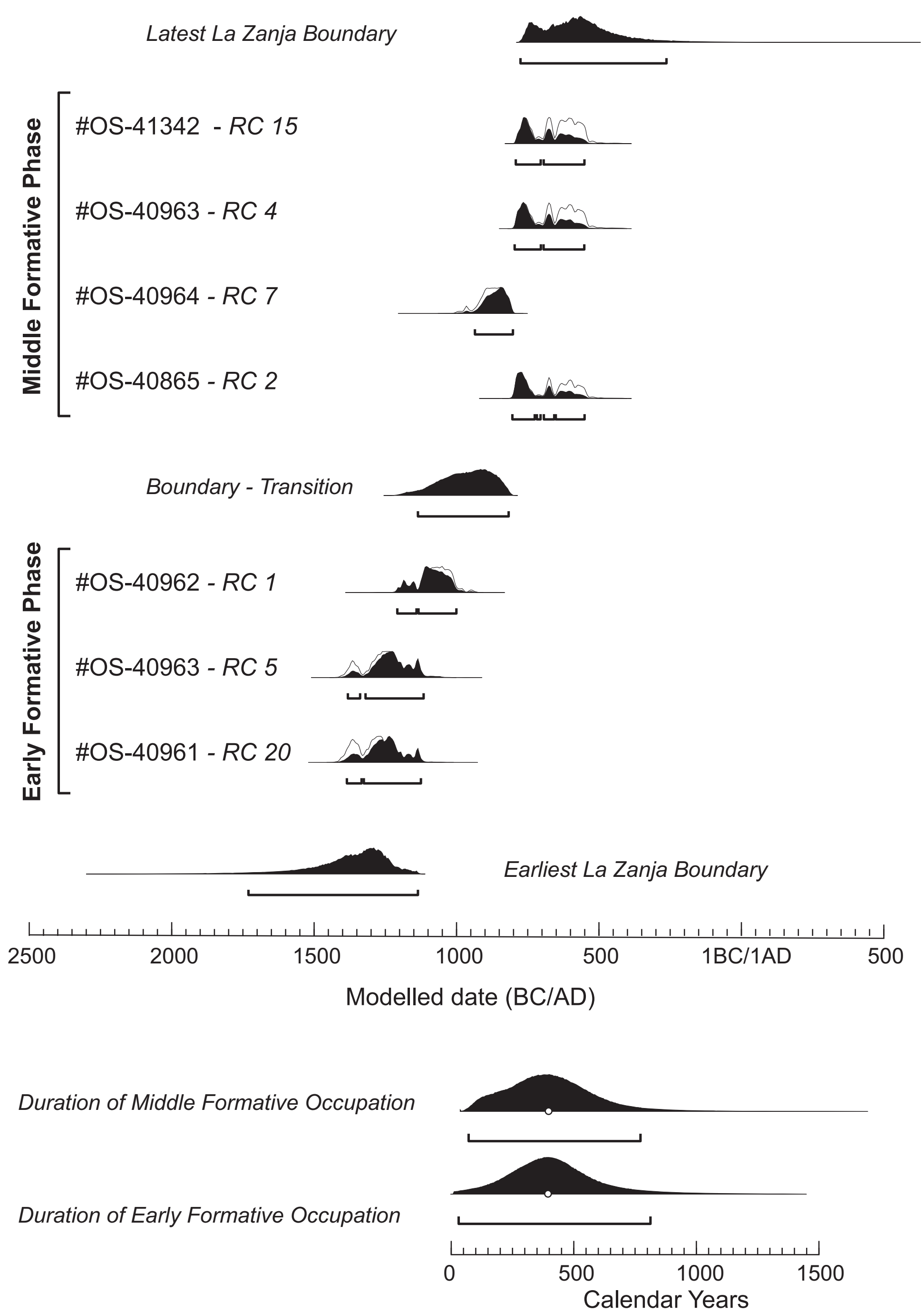

Figure 3. *Modeled calibrations for AMS ^{14}C dates at La Zanja.*

Table 1. **AMS ^{14}C dates from La Zanja used in Bayesian chronological model.**

Sequence/phase	OS #	Sample	^{14}C age (BP)	Modelled 2-σ cal range
		Boundary		784–266 BC
Middle Formative Period				
	41343	RC 15	2510 ± 30	793–551 BC
	40963	RC 4	2520 ± 35	797–552 BC
	40964	RC 7	2720 ± 40	936–803 BC
	40865	RC 2	2540 ± 40	805–551 BC
		Boundary		1134–818 BC
Early Formative Period				
	40962	RC 1	2890 ± 30	1208–1001 BC
	41342	RC 5	3010 ± 40	1382–1116 BC
	40961	RC 20	3030 ± 40	1386–1126 BC
		Boundary		1737–1134 BC

Indices were calculated for richness, diversity and evenness in the Early and Middle Formative Period shellfish assemblages. Richness was determined as a raw count of taxa present in the Early and Middle Formative assemblages. It is simply a measure of the number of shellfish taxa represented in the sub-assemblages being compared and is a product of the overall species diversity, prehistoric subsistence and processing decisions, and variations in sample size and shell preservation. Diversity was calculated using the Shannon-Weaver Index and takes into account number of species present and how evenly the numbers (MNI) are distributed among taxa (Reitz and Wing 1999:104–106). This accounts for the overall dietary contribution of each species rather than simple presence or absence. Evenness or equitability was calculated by dividing the Shannon-Weaver function by the number of species in the community. It provides a measure of how evenly distributed the abundance of taxa are in the assemblage with 1 indicating even distribution and lower values indicating the dominance of 1 or more species. This index is therefore sensitive to dietary shifts from single high-ranked prey to a greater diversity of low-ranked prey, or vice versa, through time.

RESULTS

Shellfish taxa were compared using MNI with most species divided into habitats (Table 2, Figure 4A). A total of 4702 shellfish (MNI) from La Zanja were identified from both Early and Middle Formative strata. In the Early Formative, 2,102 total shellfish (MNI) were recovered and 2,091 were identified to the species level (23 distinct species). Another 11 MNI were identified to the genus level (two additional genera identified). In the Middle Formative, shellfish remains increase to 2,600 MNI and represent a much more diverse collection of taxa with 2,562 MNI identified to 31 different species, 35 MNI identified to 5 genera, 2 MNI identified to family, and 1 MNI identified only as an unknown taxa of barnacle. Ten species dominate the La Zanja shellfish assemblage: *Chione californiensis*, *Donax punctatostriatus*, *Megapitaria auranitiaca*, *Noetia reversa*, *Ostrea palmula*, *Tagelus affinis*, *Tivela hians*, *Mytella strigata*, *Oliva incrassata*, and *Theodoxus luteofasciata.* Together these species constitute 96% of the Early Formative shellfish assemblage and 95% of shellfish remains in the Middle Formative (Figure 4B).

Table 2. **La Zanja shellfish identified taxa with MNI, preferred habitat, and average shell size.** Q6

Species	Early Formative	Middle Formative	Common name	Habitat	Typical shell length (mm)	Reference
Bivalves						
Marine						
Anadara formosa	0	1	Ark Clam	Marine offshore 11–82 m, attached to rocks	121	Keen 1971
Anadara multicostata	7	12	Many-ribbed Ark	Sandbars accessible at low tide	59	Keen 1971
Antigona multicostata	1	2		Sand and among rocks at low tide	unknown	Voorhies, personal communication 2010
Chama mexicana	0	3		Intertidal	63–101	Keen 1971
Chione californiensis	10	64	California Venus	Intertidal mudflats	68	Keen 1971
Diplodonta sericata	2	2	Flat Diplodon	Intertidal sand beaches and flats to 10 m	22 (height)	Parker 1964
Donax punctatostriatus	5	952		Marine intertidal to 5m	45	Voorhies, personal communication 2010
Euvola sp.	0	1		Marine		
Glycymeris gigantea	0	3		Offshore or intertidal	~70	Keen 1971
Lyropecten subnodosus	1	0	Pacific Lion's Paw	Marine offshore	165	Keen 1971
Megapitaria aurantiaca	92	69	Golden Callista	Tidal flats	112	Keen 1971
Noetia reversa	4	26		Intertidal and sub-tidal 73 m	37	Voorhies, personal communication 2010

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Table 2. **La Zanja shellfish identified taxa with MNI, preferred habitat, and average shell size. *(Continued)***

Species	Early For-mative	Middle Forma-tive	Common name	Habitat	Typical shell length (mm)	Reference
Ostrea palmula	78	53	California Oyster	Attached to mangrove roots or rocks, usually in areas exposed to surf up to 7 m	76	Keen 1971
Pinnidae sp.	0	2	Pen shells	Mud and gravel in quiet bays	220<	Keen 1971
Pododesmus macroschisma	1	0	Alaska Jingle	Intertidal and sub-tidal to 90 m	67	Coan et al. 2000
Tagelus affinis	10	87	Neighbor Tagelus	Mudflats or offshore to 73 m	55	Keen 1971
Tivela hians	2	67		Marine, near-shore sand	50	Voorhies, personal communi-cation 2010
Trachy-cardium consors	4	1		Tidal flats and sub-tidal to 45 m	60	Keen 1971
Tucetona multicostata	0	2		Marine offshore to 90 m	35	Keen 1971
Undulostrea megodon	0	17		Low to deep (110 m) rocky intertidal	76	Keen 1971
Estuarine						
Chione subrugosa	1	6	Semi-rough Chione	Lagoons and mudflats	42	Keen 1971
Mytella strigata	100	132	Mangrove mussel	Common in mud near mangroves.	58	Abbot and Dance 1982

(Continued on next page)

Table 2. **La Zanja shellfish identified taxa with MNI, preferred habitat, and average shell size. *(Continued)***

Species	Early Formative	Middle Formative	Common name	Habitat	Typical shell length (mm)	Reference
Polymesoda sp.	4	6		Brackish to freshwater, not sandy beach	30–60	Keen 1971
Gastropods						
Marine						
Cerithium stercusmuscarum	20	18	Cerith snails	Intertidal rocky shores	25	Parker 1964
Cymatium wiegmanni	5	2		Deep water on rocks; used by hermit crabs	76	
Hexaplex erythrostomus	3	8	Pink Murex	Intertidal; feed on *Megaptaria squalida*	101	Keen 1971
Natica chemnitzii	0	7		Intertidal mudflats and sand	33	Keen 1971
Northia northiae	0	1		Offshore	45	Voorhies, personal communication 2010
Oliva incrassata	31	151	Olivella Snail	Outer edge of sandspits at very low tides	55	Keen 1971
Semicassis sp.	0	1		Sand at low tide	50	Keen 1971
Stramonita biserialis	3	2		Rocky intertidal	75	Keen 1971
Strombus galeatus	0	2	Cortez Conch	Rocky areas at low tide and close offshore	190	Keen 1971

(Continued on next page)

Table 2. **La Zanja shellfish identified taxa with MNI, preferred habitat, and average shell size. *(Continued)***

Species	Early Formative	Middle Formative	Common name	Habitat	Typical shell length (mm)	Reference
Tripsycha sp.	0	4	Worm Snails	Marine.	80 (length of coil); 10 (diam. of opening)	Keen 1971
Turritella leucostoma	0	2		Marine, up to depths of 40 m mud and sand flats	115 (length); 20 (diam.)	Keen 1971
Estuarine						
Cerithidea mazatlanica	17	10		Incidental? Tidal flats, mudflats, and marshes	27	Keen 1971
Theodoxus luteofasciata	1,690	860		Margins of mangrove swamps and mudflats	12	Keen 1971
Marine/Estuarine						
Melongena patula	4	1	Pacific Crown Conch	Sand, mudflats, intertidal, and estuaries	117	Keen 1971
Arthropods						
Marine						
Megabalanus sp.	7	23	Barnacle	Intertidal marine on rocks		
Unknown barnacle	0	1	Barnacle	Intertidal marine on rocks		
Total MNI	2,102	2,600				
Total taxa	25	38				

We identified the habitat for each mollusk taxa based on Keen's (1971) designations for western American tropical shellfish (Table 2, Figure 4A). Seven of the ten most common species are marine clams that are found in intertidal sandy beach or mudflat habitats. Most of the following clam species are small, with shell sizes that average less than 70 mm. *Megapitaria auranitiaca* is larger with an average shell width of about

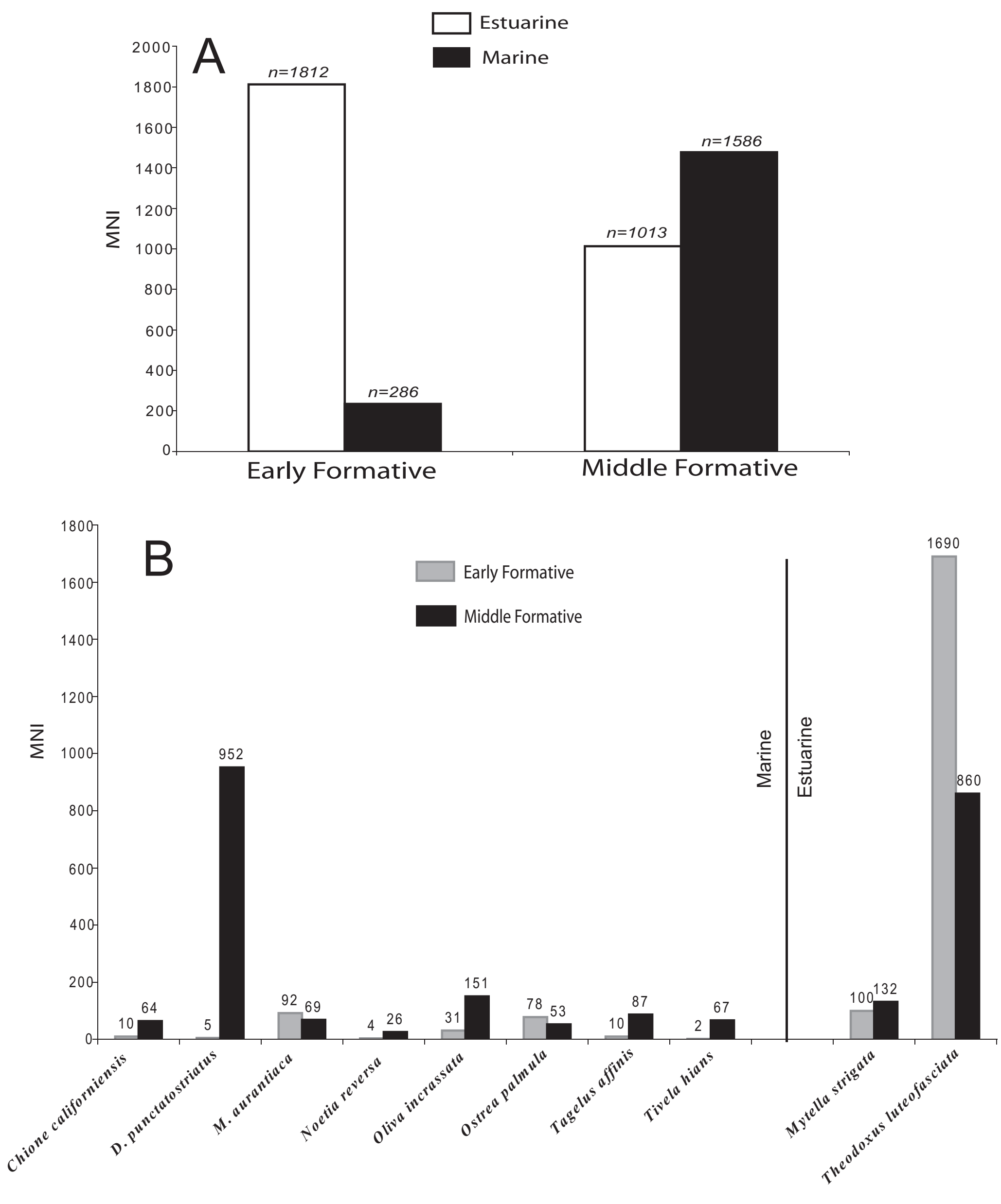

Figure 4. *A. La Zanja Early and Middle Formative Period shellfish species divided by habitat in MNI. (4B). La Zanja ten most common shellfish species Early and Middle Formative Period MNI.*

112 mm. *Chione californiensis* is found in intertidal mudflats. The clam *Donax punctatostriatus* is found in intertidal and subtidal areas up to 5 m. *Megapitaria aurantiaca*, the Golden Callista clam, is found in tidal flats. The preferred habitat for *Noetia reversa* is intertidal areas and it can also be found in subtidal habitats up to 73 m in

depth. *Tagelus affinis*, the Neighbor Tagelus is found in mudflats or offshore sand to 73 m. The clam *Tivela hians*, is found in near-shore sand. Another bivalve species that is common at La Zanja is the California oyster, *Ostrea palmula*, which attaches to mangrove roots and rocks typically in areas of tidal reach up to depths of 7 m. The Olivella snail, *Oliva incrassata* is also typically found in marine, intertidal sandy beaches, commonly found on the surface at low tides. These marine taxa were harvested either to the west or southwest of La Zanja along the barrier beach or northwest in Puerto Marqués. Both of these areas were easily accessed by watercraft from La Zanja. The dominant estuarine shellfish taxa found in the assemblage (*Theodoxus luteofasciata* and *Mytella strigata*) are both found in muddy lagoon sediments adjacent to the site.

Locally available estuarine taxa dominate the Early Formative Period assemblage (Table 2, Figure 4A; $N = 1812$, MNI). Only a small number ($N = 286$, MNI) were from marine habitats and the dominant estuarine species was a small (12-mm shell) brackish water snail (*Theodoxus luteofasciata*; N = 1690, MNI or 80% of the assemblage). There was an overall increase in shellfish exploitation during the Middle Formative Period ($N = 2600$, MNI) and the number of marine taxa jumped dramatically (1,586 of 2,600 total MNI). Richness, diversity, and evenness in the mollusk assemblage all increased from the Early to Middle Formative Period (Figure 5). *Theodoxus* declined by almost half, but the snail still represents 33% of Middle Formative shellfish assemblage. *Donax punctatostriatus*, a small marine clam species, dominates the Middle Formative assemblage ($N = 952$; 37%). Marine clam species increase overall in the Middle Formative Period deposits and all clam species from marine intertidal or mudflat habitats represent over 50% of the total assemblage. This suggests a transition through time from more local, estuarine snail gathering to a wider foraging area that included the collection of clams from marine habitats that were transported back to La Zanja from beach environments.

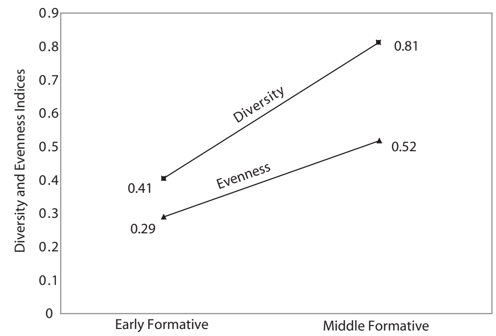

Figure 5. *Diversity and evenness values of shellfish assemblage at La Zanja from the Early to Middle Formative Period.*

DISCUSSION

The shellfish assemblage at La Zanja is taxonomically rich and composed of mollusks from different types of habitats. There are changes in the shellfish assemblage through the Formative Period that we interpret as economic reorganization as populations expanded at the site and became more dependent upon maize-based food production (Kennett et al. 2008). This may have resulted from the depression of locally available resources or increases in the economical viability of mollusks from more distant marine habitats because of improved watercraft. Although the sample is small it represents a first glimpse of subsistence changes between the Early and Middle Formative Periods and provides a starting point for testing these hypotheses in the future with additional work at the site.

Based on the available data we argue that decreases in the number of estuarine shellfish in the Middle Formative at La Zanja indicate local depletion resulting from population-dependent increases in human predation. A marine species that was minimally present in the Early Formative assemblage, *Donax punctatostriatus*, became the most common species in the Middle Formative. This occurred as the most dominant Early Formative estuarine species

(*Theodoxus luteofasciata*) was reduced to over half its former abundance. The collection of this marine species at more distant locations may have been enhanced by the availability of watercraft. There was an increased focus in the Middle Formative on bivalve clam species from sandy and mudflat intertidal zones. The two most common shellfish species in the Early Formative, the estuarine gastropod *Theodoxus luteofasciata* and the brackish water mussel *Mytella strigata*, are both perching species that would be easily located and collected in large numbers from the surface of sand, rocks, or mangrove roots. These species would require little skill or time to find and gather compared with the burrowing clam species that make up over 50% of the Middle Formative shellfish assemblage.

Small species such as aquatic gastropods individually represent a small energetic return, but require little skill to collect in large quantities. These gastropods were also easy to process by crushing in large quantities or boiling, as demonstrated ethnographically and archaeologically in other areas (Raab 1992; Voorhies 2004). Although the mollusk assemblage is well preserved these gastropods all show evidence for cracking for meat extraction. Most of the marine shellfish species evident in the Middle Formative deposits were mudflat or intertidal clams and have larger meat packages than the estuarine snail. Large tidal flat bivalves require more expertise and time to locate and harvest because they burrow in the sand (Raab 1992), although technologies such as rakes may have been used to reduce time and effort. Clam meat can be dried and stored for long periods of time. The handling and transportation costs of acquiring marine mollusks from more distant locations places limits on the taxa pursued and how they were processed (Bird and Bliege Bird 1997). If watercraft were more limited in the Early Formative Period, then extensive field processing (e.g., removal of shells, drying; Bird and Bliege Bird 1997) would have been necessary to generate viable load sizes exceeding the energy expended in transport biasing the assemblage towards underrepresentation of shellfish remains (Bird et al. 2002). The marine mollusks in the Middle Formative assemblage, on the other hand, are the largest available along the coast and larger than locally available snails therefore this is consistent with the prey choice model prediction that larger species will be targeted as transport costs increase. However, the dominance of marine mollusks at La Zanja from more distant locations during the Middle Formative points to changes in transportation costs consistent with the availability of more viable watercraft (see below).

The overall quantity of shellfish increased in the assemblage from the Early Formative (MNI = 2098) to the Middle Formative (MNI = 2599), perhaps indicating a higher level of predation pressure as human populations rose in the village (Table 2, Figure 4A). Shellfish increased in diversity and evenness during the Middle Formative (Figure 5) suggesting expanding diet breath in the face of population-dependent resource depression locally. Larger shellfish were also collected at more distant locations and transported back to La Zanja. This suggests that people were searching farther and longer for prey during the Middle Formative. If watercraft were used more in the Middle Formative, this could increase foraging efficiency, as these early farmers could cover more ground and easily return with materials from more distant resource patches (Gomez et al. 2011; Thomas 2008). A rise in the use of boats might negate the importance of removing low-utility parts (shell) prior to transport of shellfish back to central places (Ames 2002). More marine shell in the Middle Formative assemblage is expected if boats were used for the transport of goods more frequently than in the Early Formative. However, if marine shellfish were transported primarily on foot in both periods they may be underrepresented in both assemblages and more important dietary constituents than faunal remains indicate (Bird et al. 2002).

There is evidence for increased maritime trade along the Pacific Coast during the latest Early Formative and earliest Middle Formative Periods (Gomez et al. 2011). There is also evidence for the development of more intensive trade networks with the Pacific Coast Olmec either over land or across the

Isthmus of Tehuantepec and up and down the Pacific Coast. Lagoons and coastal river systems served as important flat-water conduits for boats carrying pottery, obsidian, and other valuable resources. White slipped and incised pottery became more prevalent in the assemblage at La Zanja during the Middle Formative along with other status items suggesting linkages/contact with the Gulf Coast Olmec. It is likely that watercraft were commonly used at this time both for the transport of long-distance trade goods and for local travel. If transportation via watercraft became more common in the Middle Formative, there may have been less incentive to process mollusks before transport, consistent with the higher incidence of low-utility shell from marine invertebrates in the La Zanja Middle Formative component. As populations increased during the Middle Formative, the use of watercraft might have served as a cost-reduction strategy in the face of resource depression, since travel costs to more distant patches would be reduced. It is also possible that marine mollusks were obtained via trade with coastal communities. Agricultural productivity was higher on the more expansive alluvial portions of the coast compared with barrier beach locations and maize, beans, and squash could have been exchanged for marine foods including shellfish. Trade and the production of trade items to exchange for food provides another mechanism for expanding dietary breadth (Kennett 2005). Regardless, changes in the La Zanja shellfish assemblage through time are generally consistent with the prey choice model and Marginal Value Theorem for dietary expansion in the face of population-dependent resource depression.

CONCLUSION

The Formative Period occupants of La Zanja combined the cultivation of domesticated plants with a heavy reliance upon coastal and estuarine resources, largely shellfish and fish. Foraging strategies changed and diet breadth expanded to incorporate a larger array of shellfish taxa as people became more reliant on maize-based food production and village populations increased during the Middle Formative Period. Mollusks were also collected from more distant beach habitats and transported back to La Zanja. This parallels an increased reliance upon boats for trade evident along with coasts of Mesoamerica during the Formative Period (Gomez et al. 2011). The predictions of OFT models are consistent with many of the patterns seen in the shellfish assemblage at La Zanja where the increase in shellfish catchment area in the Middle Formative seems to occur at a time of population expansion and increasing human environmental impacts with a growing commitment to maize agriculture.

While our examination of shellfish exploitation and expanding diet breadth at La Zanja predict a more generalized diet and a movement of foragers into more distant habitats, with decreasing encounter rates with local high-ranked prey (Broughton and Bayham 2003; Broughton and O'Connell 1999; Hawkes and O'Connell 1992), parallel shifts in diet breadth might also be explored through changes in other aquatic taxa (fish, turtles, etc.). Our previous work suggests the local depression of nesting sea turtle populations at this and other locations through time (Smith et al. 2007) that is consistent with expanding human populations regionally. Future work will focus on analysis of fish taxa and other faunal classes (e.g., large mammals) in order to rank prey species and examine changes in foraging patterns that may have existed at La Zanja. Through an examination of a larger zooarchaeological assemblage, optimal foraging models from behavioral ecology provide an effective tool for exploring the ecological effects of population growth and human predation within coastal settings.

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REFERENCES

Abbott, R. T. and S. P. Dance. 1982. *Compendium of Seashells: A Color Guide to More than 4,200 of the World's Marine Shells*. New York: E. P. Dutton.

Ames, K. M. 2002. Going by boat: The forager-collector continuum at sea. In *Beyond Foraging and Collecting: Evolutionary Change in Hunter-Gatherer Settlement Systems* (B. Fitzhugh B. and J. Habu, eds.):17–50. New York: Kluwer/Plenum Press.

Ames, K. M. and H. D. G. Maschner. 1999. *Peoples of the Northwest Coast: Their Archaeology and Prehistory*. New York: Thames and Hudson.

Bird, D. W. and R. L. Bliege Bird. 1997. Contemporary shellfish gathering strategies among the Meriam of the Torres Strait Islands, Australia: Testing predictions of a central place foraging model. *Journal of Archaeological Science* 24:39–63.

Bird, D. W., J. L. Richardson, P. M. Veth, A. J. Barham. 2002. Explaining shellfish variability in Middens on the Meriam Islands, Torres Strait, Australia. *Journal of Archaeological Science* 29:457–469.

Braje, T. J., D. J. Kennett, J. M. Erlandson, and B. J. Culleton. 2007. Trans-Holocene subsistence changes and human impacts on a marine ecosystem on Santa Rosa Island, California. *American Antiquity* 72(4):735–756.

Bronk Ramsey, C. 2013. OxCal v. 4.2. Retrieved from https://c14.arch.ox.ac.uk/login/login.php?Location=/oxcal/OxCal.html.

Broughton, J. M. and F. E. Bayham. 2003. Showing off, foraging models, and the ascendance of large game hunting in the Middle Archaic. *American Antiquity* 68(4): 783–789.

Broughton, J. M. and J. F. O'Connell. 1999. On evolutionary ecology, selectionist archaeology, and behavioral ecology. *American Antiquity* 64(1):153–165.

Brush, C. F.1969. *A contribution to the archaeology of coastal Guerrero, Mexico*. Ph.D. Dissertation. New York: Columbia University.

Claassen, C. L. 1986. Temporal patterns in marine shellfish-species use along the Atlantic coast in the southeastern United States. *Southeastern Archaeology* 5:120–137.

Clark, J. E. and M. Blake. 1994. Power and prestige: Competitive generosity and the emergence of rank in lowland Mesoamerica. In *Factional Competition and Political Development in the New World* (E. M. Brumfiel and J. W. Fox, eds.):17–30. Cambridge: Cambridge University Press.

Coan, E. V., P. V. Scott, F. R. Bernard. 2000. *Bivalve seashells of western North America: Marine bivalve mollusks from Arctic Alaska to Baja California*. Santa Barbara Museum of Natural History Monographs, Studies in Biodiversity: no. 2. Santa Barbara: Museum of Natural History.

Cyphers, A. 1996. Reconstructing Olmec life at San Lorenzo. In *Olmec Art of Ancient Mexico*, edited by (E. P. B. Benson, B. de la Fuente, and M. Castro-Leal, eds.):61–71. Washington, DC: National Gallery of Art.

Cyphers, A., T. Murtha, J. Borstein, J. Zurita-Noguera, R. Lunagómez, S. Symonds, G. Jiménez, M. Arturo Ortiz, and J. M. Figueroa. 2007–2008. Arqueología digital en la primera capital olmeca, San Lorenzo. *Thule* 22–25: 121–144.

de Boer, W. F., T. Pereira, and A. Guissamulo. 2000. Comparing recent and abandoned shell middens to detect the impact of human exploitation on the intertidal ecosystem. *Aquatic Ecology* 34:287–297.

Doolittle, W. E. 1990. *Canal Irrigation in Prehistoric Mexico: The Sequence of Technological Change*. Austin: University of Texas Press.

Erlandson, J. M. 1988. The role of shellfish in prehistoric economies: A protein perspective. *American Antiquity* 53:102–109.

Erlandson, J. M. 2001. The archaeology of aquatic adaptations: Paradigms for a new millennium. *Journal of Archaeological Research* 9: 287–350

Erlandson, J. M., T. J. Braje, T. C. Rick, N. P. Jew, D. J. Kennett, N. Dwyer, and J. Watts. 2011. 10,000 years of human predation and size changes in the owl limpet (Lottia gigantea) on San Miguel Island, California. *Journal of Archaeological Science* 38: 1127–1134.

Erlandson, J. M. and T. C. Rick. 2008. Archaeology, marine ecology, and human impacts on marine environments. In *Human Impacts on Ancient Marine Ecosystems* (T. C. Rick and J. M. Erlandson, eds.):1–20. Berkeley: University of California Press.

Erlandson, J. M., T. C. Rick, and R. Vellanoweth. 2004. Human impacts on ancient environments: A case study from California's Northern Channel Islands. In *Voyages of Discovery: the Archaeology of Island* (S. M. Fitzpatrick, ed.):51–84. Westport: Praeger.

Flannery, K. V. 1973. The origins of agriculture. *Annual Review of Anthropology* 2:271–310.

Flannery, K. V. 1986. *Guila Naquitz: Archaic Foraging and Early Agriculture in Oaxaca, Mexico*. Orlando: Academic Press Inc.

Flannery, K. V. and J. Marcus. 2000. Formative Mexican chiefdoms and the myth of the "Mother Culture". *Journal of Anthropological Archaeology* 19:1–37.

Glassow, M. A. and L. R. Wilcoxon. 1988. Coastal adaptations near Point Conception California, with particular regard to shellfish exploitation. *American Antiquity* 53:36–51.

Gomez, J., D. J. Kennett, H. Neff, M. D. Glascock, and B. Voorhies. 2011. Early formative pottery production, mobility, and exchange on the Pacific Coast of Southern Mexico. *Journal of Island and Coastal Archaeology* 6:333–350.

Hawkes, K. and J. F. O'Connell. 1992. On optimal foraging models and subsistence transitions. *Current Anthropology* 33(1):63–66.

Hawkes, K., J. F. O'Connell, and L. Rogers. 1997. The behavioral ecology of modern hunter gatherers, and human evolution. *Trends in Ecology and Evolution* 12:29–32.

Hooke, R. L., 2000. On the history of humans as geomorphic agents. *Geology* 28:843–846.

Kaplan, H. and K. Hill. 1992. The evolutionary ecology of food acquisition. In *Evolutionary Ecology and Human Behavior* (E. A. Smith and B. Winterhalder, eds.):167–201. New York: Walter de Gruyter.

Keen, A. M. 1971. *Seashells of Tropical West America: Marine Mollusks from Lower California to Peru*. Stanford: Stanford University Press.

Kennett, D. J. 2005. *The Island Chumash: Behavioral Ecology of a Maritime Society*. Berkeley: University of California Press.

Kennett, D. J. 2012. Archaic Period Foragers and Farmers in Mesoamerica. In *Oxford Handbook of Mesoamerican Archaeology* (D. L. Nichols and C. A. Pool eds.):141–150. Oxford: Oxford University Press.

Kennett, D. J., B. J. Culleton, B. Voorhies, and J. R. Southon. 2011. Bayesian analysis of high precision AMS ^{14}C dates from a Prehistoric Mexican shellmound. *Radiocarbon* 53(2):101–116.

Kennett D. J. and B. Voorhies. 1996. Oxygen isotopic analysis of archaeological shells to detect seasonal use of wetlands on the southern Pacific coast of Mexico. *Journal of Archaeological Science* 23:689–704.

Kennett, D. J., B. Voorhies, J. Iriarte, J. G. Jones, D. Piperno, M. T. Ramírez Herrera, and T. A. Wake. 2004. Avances en el Proyecto Arcaico-Formativo: Costa de Guerrero. Estregado al Instituto Nacional de Antropología e Historia. Manuscript in possession of D. J. Kennett, Guerrero, Mexico.

Kennett, D. J., B. Voorhies, and D. Martorana. 2006. An ecological model for the origins of food production on the Pacific coast of southern Mexico. In *Behavioral Ecology and the Transition to Agriculture* (D. J. Kennett and B. Winterhalder, eds.):103–136. Berkeley and Los Angeles: University of California Press.

Kennett, D. J., B. Voorhies, T. A. Wake, and N. Martínez. 2008. Human impacts on marine ecosystems in Guerrero, Mexico. In *Human Impacts on Marine Ecosystems* (T. C. Rick and J. M. Erlandson, eds.):103–124. Berkeley: University of California Press.

Kennett, D. J., B. Winterhalder, J. Bartruff, and J. M. Erlandson. 2009. An ecological model for the emergence of institutionalized social hierarchies on California's Northern Channel Islands. In *Pattern and Process in Cultural Evolution* (S. Shennan, ed.):69–80. Berkeley: University of California Press.

Klein, R. G., G. Avery, K. Cruz-Uribe, D. Halkett, J. E. Parkington, T. Steele, T. P. Volman, and R. Yates. 2004. The Ysterfontein 1 Middle Stone Age site, South Africa, and early human exploitation of coastal resources. *Proceedings of the National Academy of the Sciences* 101:5708–5715.

Lentz, D. L. 2000. Anthropocentric food webs in the precolumbian Americas. In *Imperfect Balance: Landscape Transformations in the Precolumbian Americas* (D. L. Lentz, ed.):89–119. New York: Columbia University Press.

Madsen, D. B. and D. N. Schmitt. 1998. Mass collecting and the diet breadth model: A Great Basin example. *Journal of Archaeological Science* 25:445–455.

Mannino, M. A. and K. D. Thomas. 2002. Depletion of a resource? The impact of prehistoric human foraging on intertidal mollusc communities and its significance for human settlement, mobility and dispersal. *World Archaeology* 33(3):452–474.

Manzanilla López, R. A. 2000. *La Region Arqueológica de la Costa Grande de Guerrero: Su Definición a través de la Organización Social y Territorialidad Prehispánicas*. Ph.D. Dissertation. México City: Escuela Nacional de Antropología e Historia.

Manzanilla López, R. A., A. Talavera González, and E. Rogriguez Sanchez. 1991. *Informe Técnico de Campo de la Primavera Etapa del Proyecto de Investigación y Salvamento Arqueológico en Puerto Marquéz, Estado Guerrero*. México City: Entregado al INAH Mexicanos y Centroamericanos, Gobierno del Estado de Guerrero and Instituto Nacional de Antropología e Historia.

Milner, N., Barrett, J., and Welsh, J. 2007. Marine resource intensification in Viking Age Europe:

the molluscan evidence from Quoygrew, Orkney. *Journal of Archaeological Science* 34:1461–1472.

Nagaoka, L. 2002. Explaining subsistence change in southern New Zealand using foraging theory models. *World Archaeology* 34(1):84–102.

Parker, R. H. 1964. Zoogeography and ecology of macro-invertebrates of the Gulf of California and continental slope of Western Mexico. In *Marine Geology of the Gulf of California: A Symposium* (T. H. van Andel and G. G. Shor, Jr., eds.):331–376. The American Association of Petroleum Geologists, Memoir 3.

Piperno, D. R. 2006. The origins of plant cultivation and domestication in the neotropics. In *Behavioral Ecology and the Transition to Agriculture* (D. J. Kennett and B. Winterhalder, eds.):137–166. Berkeley and Los Angeles: University of California Press.

Raab, M. 1992. An optimal foraging analysis of prehistoric shellfish collecting on San Clemente Island, California. *Journal of Ethnobiology* 12:63–80.

Reitz, E. J. and E. S. Wing, 1999. *Zooarchaeology*. Cambridge: Cambridge University Press.

Rick, T. C. and J. M. Erlandson. 2009. Coastal exploitation. *Science* 325:952–953.

Rick, T. C., J. M. Erlandson, R. L. Vellanoweth, and T. J. Braje. 2005. From Pleistocene mariners to complex hunter-gatherers: The archaeology of the California Channel Islands. *Journal of World Prehistory* 19:169–228.

Rosenswig, R. M. 2009. *The Beginnings of Mesoamerican Civilization: Inter-Regional Interaction and the Olmec*. Cambridge: Cambridge University Press.

Smith, B. D. 2001. Low-level food production. *Journal of Archaeological Research* 9(1): 1–43.

Smith, C. B., D. J. Kennett, T. A. Wake, and B. Voorhies. 2007. Prehistoric sea turtle hunting on the Pacific coast of Mexico. *Journal of Island & Coastal Archaeology* 2(2):231–235.

Smith, E. A. 1983. Anthropological applications of optimal foraging theory: A critical review. *Current Anthropology* 24(5):625–640.

Stephens, D. W. and J. R. Krebs. 1986. *Foraging Theory*. Princeton: Princeton University Press.

Thacker, H. B. 2011. Intensification of shellfish exploitation: evidence of species-specific deviation from traditional expectations. *Journal of Archaeological Science* 38: 2596–2605.

Thomas, D. H. 2008. *Native American Landscapes of St. Catherines Island, Georgia: Theoretical Framework*. New York: American Museum of Natural History, Anthropologicial Papers, Number 88.

Voorhies, B. 1996. The transformation from foraging to farming in lowland Mesoamerica. In *The Managed Mosaic: Ancient Maya Agriculture and Resource Use* (S. L. Fedick, ed.):17–29. Salt Lake City: University of Utah Press.

Voorhies, B. 2004. *Coastal Collectors in the Holocene: The Chantuto People of Southwest Mexico*. Gainesville: University Press of Florida.

Webster, D. 2002. *The Fall of the Ancient Maya*. London: Thames and Hudson.

Winterhalder, B. and D. J. Kennett. 2006. Behavioral ecology and the transition from hunting and gathering to agriculture. In *Behavioral Ecology and the Transition to Agriculture* (D. J. Kennett and B. Winterhalder, eds.):1–21. Berkeley and Los Angeles: University of California Press.

Winterhalder, B., D. J. Kennett, M. Grote, and J. Bartruff 2010. A Bayesian approach to ideal free settlement on California's Northern Channel Islands. *Journal of Anthropological Archaeology* 29:469–490.

Winterhalder, B. and E. A. Smith. 2000. Analyzing adaptive strategies: Human behavioral ecology at twenty-five. *Evolutionary Anthropology* 9:51–72.

Yesner, D. R. 1980. Maritime hunter-gatherer ecology and prehistory. *Current Anthropology* 21(6):727–750.

Zeanah, D. W. 2004. Sexual division of labor and central place foraging: A model for the Carson Desert of western Nevada. *Journal of Anthropological Archaeology* 23:1–32.