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The forest and the trees: Small-scale ecological variability and archaeological interpretations of temporal changes in California mussel shell size

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ABSTRACT

As global efforts to understand and document anthropogenic impacts on the coastal environment have increased, so have archaeologists' eagerness to contribute relevant research. Our publication (Thakar et al., 2017) sought to enhance scientific rigor in archaeological evaluation of potential anthropogenic impacts on past shellfish communities through ecological assessment of small scale-variability in California mussel growth rates and through development of an alternative working hypothesis. In response to comment by Braje et al (2017) we offer additional explanation in support of our experimental design, targeted tidal foraging hypothesis, and methods of evaluation. We argue that in order to fully understand adaptations (or impacts) of prehistoric coastal foragers, archaeologists must embrace a nuanced view of how people dealt with small-scale ecological variability.

1. Introduction

Firmly grounded in optimal foraging theory, ethnographic observation, and robust ecological data, the primary argument of our research article, “Reconsidering evidence of human impacts: Implications of within-site variation of growth rates in *Mytilus californianus* along tidal gradients,” is that small-scale ecological variation in intertidal environments influenced prehistoric coastal foraging behavior and mediated human-environmental interactions with (and impacts on) intertidal marine resources (Thakar et al., 2017). Although we challenge arguments that increased intensity of shellfish collection led to resource depression on the Northern California Channel Islands, we do not reject this hypothesis. Rather, our over-arching premise is intended to enhance scientific rigor in archaeological assessment of potential anthropogenic impacts on past shellfish communities. In this spirit, we propose an alternative working hypothesis that considers the influence of tidal regime on human intertidal foraging behavior and resultant archaeomalacological assemblages.

In their comment, “The forest or the trees: Interpreting temporal changes in California mussel shell size,” Braje et al., 2017 identify four primary concerns: (1) the experimental design of our ecological study, (2) the value of untested hypotheses, (3) the archaeological implications of intertidal foraging behaviors and (4) the use of oxygen isotope data in evaluation of the proposed hypothesis. These concerns led Braje et al., 2017 to “offer caution when interpreting the implications” of our ecological study. We respond here to issues raised by three leading California archaeologists and offer additional explanation in support of our thesis.

1.1. Experimental design

Our robust experimental design, based on dozens of similar ecological experiments (e.g. Menge et al., 1997; Phillips, 2005; Blanchette et al., 2006a,b), purposefully controlled for predation and annual sea surface temperature (SST) variation (among other variables) in order to allow independent evaluation of the two test variables (site location and tide level). We employed cages to secure transplanted mussels until they reattached to the rocky substrate. We later loosened the cages but left them in place in order to protect the mussels from natural predators. The exclusion of predators allowed us to focus entirely on the effects of variation in

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water temperature and subaerial exposure as a result of elevation within the intertidal zone (for within-site comparisons) and the effects of variation in water temperature as a result of exposure to different oceanographic currents (for between-site comparisons). The eleven-month study encompassed both the highest and lowest SSTs of the annual cycle. We intentionally designed the duration of the experiment to control for the known effect of annual SST variation on mussel growth and to take advantage of the lowest daytime tides for transplanting, monitoring, and subsequently collecting the mussels from the lowermost reaches of the intertidal zone. In our experimental design, we anticipated high mortality (common in mussel transplants) and transplanted more mussels than required for the study in order to ensure a sufficiently large surviving population for statistical evaluation. Although the experiment suffered losses, the final sample size was valid and appropriate for the statistical tests we selected.

The results of our study demonstrate a widely known and accepted ecological phenomenon documented by many researchers (e.g. Paine, 1974; Yamada and Peters, 1988; Yamada and Dunham, 1989; Dittman and Robles, 1991; Suchanek, 1992; Hofmann and Somero, 1995; Roberts et al., 1997; Marsden and Weatherhead, 1999; Blanchette et al., 2006a; Helmuth et al., 2006; Fitzgerald-Dehoog et al., 2012; Connor and Robles, 2015). Site location and shore level have significant effects on mussel growth rates. The results of our study reinforce these general findings and provide a quantitative assessment of variation across the island environment (i.e. between sites) and across the tidal gradient (within site) on Santa Cruz Island. Given the difficult task of interpreting how past human behaviors may have shaped archaeological mussel size distributions, it is especially important for archaeologists to have a clear understanding of pervasive ecological variability in mussel growth rates known to exist in the complete absence of human foraging. Our experimental data have the potential to refine archaeologists' understanding and assessment of mussel size distribution as a measure of anthropogenic impacts on the Northern Channel Islands.

1.2. *Assumptions & hypotheses*

We argue, based on previous studies and the results of the ecological study presented in our article that local variability between site locations matters, even across a single island. Moreover, local spatial variability could be exacerbated by diachronic variation. Flores Fernandez (2017) demonstrates that some local intertidal environmental differences are stable through time and are thus unlikely to be averaged out through time. This finding resonates with our data, which demonstrates significant local variation (between sites) likely due to the effects of dynamic nearshore oceanographic patterns. Such small scale variations undoubtedly persist at large temporal scales and have the potential to bias or distort results at large spatial scales. Building on this foundation, we assert that the inference that observed paleo-mussel shell size decrease necessarily represents resource depression must rest on a critical evaluation of, or control for, the full range of environmental influences on mussel growth rates. This is necessary even (or rather especially) when researchers feel certain that potential local effects may be limited.

Although, in the past, archaeologists discounted the effect of small-scale ecological variability, the data that we present demand consideration. Based on several ethnographic studies of intertidal foraging behavior (Kingsford et al., 1991; Bird and Bliege Bird, 2000; Bleige Bird and Bird, 2002; De Boer et al., 2002; Bird et al., 2004; Rius and Cabral, 2004; Jimenez et al., 2011; Aswani et al., 2014), and the expectations of optimal foraging theory we formulate an alternative working hypothesis for the interpretation of observed decrease in mussel shell size. We propose that targeted tidal harvesting of larger mussels during low tides and spring tides gave way to daily harvesting of smaller mussels at higher shore levels during higher tides and neap tides as increasing circumscription and coastal sedentism required more regular shellfish exploitation. If our argument is valid and all of the island's inhabitants engaged in targeted tidal foraging prior to circumscription and sedentism, it certainly could result in an island-wide archaeological pattern. However, this targeted tidal foraging hypothesis is just one of the many ways in which small-scale ecological variation in mussel growth rates could influence human foraging behavior and archaeological assemblages across the Northern Channel Islands.

Our novel hypothesis, and any others that examine natural causes of variation in mussel growth rates across the island environment, do not exclude consideration of human impacts on mussel populations. Rather, we stress that multiple working hypotheses are necessary to evaluate fully the relative importance of anthropogenic versus environmental influences structuring archaeological shellfish assemblages. A strong argument for prehistoric human impacts must be constructed through exhaustive evaluation of alternative hypotheses.

1.3. *Intertidal foraging behavior & archaeological expectations*

We contend that in order to fully understand coastal adaptations of hunter-gatherers, archaeologists must embrace a nuanced view of how people deal with (and dealt with in the past) temporal and spatial variability in resource distribution, abundance, and quality. From optimal foraging theory we derive the expectation that during tides that are low enough (i.e., spring tides) collectors should exploit shellfish resources that maximize energy/effort, in this case, the larger mussels aggregated and easy-to-access in the exposed lower reaches of the intertidal zone. As large, faster-growing mussels in the lower intertidal zone inevitably start out as small mussels, we also expect individuals of all sizes to be present in this portion of the intertidal zone. The critical point here is that mussels range to larger sizes in the lower intertidal than in the upper intertidal, effectively increasing the potential harvest value of the lower intertidal zone. However, even highly selective collectors would inevitably collect smaller mussels along with the larger ones due to intermingling of byssal threads. Therefore, we clarify that low tide and spring tide catches should include greater quantities of larger mussels, but they may also include a mixture of other sizes. Based on these expectations, we argue that early island foraging peoples should have favored collecting lower intertidal mussels, particularly if human populations were not as large (i.e., living in lower density) as they were during the late Holocene.

Milliken and Johnson recently estimated that San Miguel Island's population at the time of initial contact with the Spanish explorers was about 100 people (John Johnson, personal communication, 2016). Although Paleocoastal peoples occupied a much larger island, existing data do not indicate that their population was much larger than this estimate; in fact, it could have been smaller. With such an open landscape, central-place foraging models support the expectation that highly mobile populations likely foraged over broad areas mapping onto resource patches (i.e., intertidal zones) and depositing remains/refuse in proximity to targeted locations. We expect that this Paleocoastal/Early Holocene pattern of foraging behavior should create separate sites across the island landscape, each with constituents that reflect exploitation of local resources. That is to say that shell middens located along the Paleo- or early Holocene shorelines should reflect the local conditions of the adjacent intertidal zone as well as human foraging behavior (i.e., targeted tidal foraging). Early coastal foragers who occupied coastal locations periodically during different seasons of the year or during different seasons from year to year were certainly capable of predicting and targeting low tides for intertidal foraging across the island landscape. In contrast, this expectation would not hold for shell middens located away from the ancient coast. Thakar (2016) demonstrates persistent spatial variation in the size of California mussel transported relatively short distances (~3 km) across the island landscape. Late Holocene foragers preferentially carried significantly larger mussels away from the coast towards the interior of the island. This introduces yet another critical variable into assessments of variation in mussel size distributions. The specific characteristics of the midden constituents matter, but so does midden location. We expect proximity to the resource patch to influence the size of mussel incorporated into the archaeological deposits. Our tidal foraging hypothesis focuses on patterns expected at coastal locations before and after Late Holocene population infilling and circumscription.

Braje et al., 2017 juxtapose archaeological mussel size distributions from an Early Holocene site (SMI-522) and a Late Holocene site (SMI-232) from San Miguel Island as evidence for resource depression. We argue that the mussel size distributions from these two sites do not contradict the archaeological expectations for targeted tidal foraging behavior and may actually reflect local ecological variation, targeted tidal foraging, or both. Occupations at SMI-522 and SMI-232 occurred about 7000 years apart, during a time when sea levels were rising rapidly. San Miguel Island was becoming smaller and sea-surface temperatures were warming over this period of time. The two sites are located on different portions of the island, and their adjacent intertidal zones may have differed significantly from each other. It is possible that the difference in mean mussel size illustrated by Braje et al., 2017 reflects differing local conditions, changing conditions over time, or both. In other words, changes in mussel size necessarily reflect differences in local conditions as well as possible differences in human foraging intensity. Our paper urges researchers to investigate and control for variation in local conditions as a part of constructing effective arguments regarding potential human impacts.

1.4. Methods for evaluating tidal foraging hypothesis

In order to facilitate evaluation of our targeted tidal foraging hypothesis, we presented three recommendations that could aid researchers interested in determining whether variation in shellfish assemblages might be attributed to small scale ecological variation in mussel growth rates and size zonation. Following Jerardino (2014) and Langejans et al. (2012) we argue that changing frequencies of mollusc species available at different heights in the intertidal zone provides a proxy measure for identifying potential tidal signatures. In addition to species assessments, we also suggest that oxygen isotope analysis could be used to evaluate (1) the tidal elevation of mussels recovered from the same stratigraphic context *sensu* Rick et al. (2006), and (2) the relative proportion of faster-growing individuals versus slower growing individuals recovered from the same stratigraphic context. These suggestions focus oxygen isotope analysis on assessment of where the mussels grew in the intertidal zone and how quickly they grew relative to other individuals in the same stratigraphic context. Researchers can infer where in the intertidal zone mussels grew based on the contemporaneous harvest of mussels from colder waters and mussels (or other taxa) from warmer waters at the same location. Relatively greater quantities of individuals harvested from colder waters (at the same site, during the same period of occupation) than individuals harvested from warmer waters would support targeted tidal foraging of the lower intertidal zone. The reverse pattern would be expected later in time if targeted tidal foraging gave way to more regular, daily foraging at higher tidal levels. We expect that relatively greater quantities of individuals would be harvested from warmer waters (at the same site, during the same period of occupation) than individuals harvested from colder waters. Researchers can assess how quickly mussels grew based on variation in the annual SST cycle recorded by each individual shell. Assuming that the oxygen isotope samples were collected at standardized intervals, more rapid increases and decreases in SST (a "saw-tooth" pattern *sensu* Glassow et al., 2012), indicate that the mussel was relatively slower-growing. In contrast, more smooth sinusoidal increases and decreases in SST, indicate that the mussel was relatively faster-growing. If people preferentially targeted faster-growing mussels from the lower intertidal zone, we would expect a greater proportion of shells with reconstructed annual SST cycles that demonstrate smooth sinusoidal increases and decreases in SST than shells with reconstructed annual SST cycles that demonstrate rapid "saw-tooth" increases and decreases in SST. However, we would expect the reverse pattern in later assemblages if targeted tidal foraging gave way to more regular foraging of slower growing individuals at higher tidal levels. That is to say we would expect a greater proportion of shells with reconstructed annual SST cycles that demonstrate rapid "saw-tooth" increases and decreases in SST than shells with reconstructed annual SST cycles that demonstrate smooth sinusoidal increases and decreases in SST.

For evaluation of where and how quickly mussels grew, it is not necessary to determine season of harvest or infer relative degree of sedentism. In fact, season of harvest is likely a poor test of targeted tidal foraging. Both neap tides and spring tides occur within a single lunar cycle. Even with high instrument precision (i.e. ±0.05‰ for $\delta^{18}O$) and strongly patterned seasonal variability in SST, confident seasonal attribution rarely exceeds 2–3 month intervals (e.g., Jew et al., 2013a,b, 2014; Jew and Rick, 2014; Thakar, 2014). Thus, existing oxygen isotope data from the Santa Barbara Channel Region lack the precision required to determine whether California mussel shells were harvested at the monthly and sub-monthly intervals relevant for assessing tidal regimes.

The silver lining here is that Braje et al., 2017 may have access to isotopic data that could be used to evaluate tidal elevation and relative growth rates of mussels from archaeomalacological assemblages previously hypothesized to represent resource depression. Testing our hypothesis requires that: (1) the oxygen isotope data represent a complete annual SST cycle for each individual mussel shell, and (2) that the oxygen isotope samples were collected at standardized intervals along the primary growth axis for each individual mussel shell. If these conditions are met, and the data are available for multiple shells per stratigraphic context, Braje et al., 2017 should be able to empirically evaluate whether our targeted tidal foraging hypothesis is supported. By extension, testing and ruling out alternative hypotheses (using the methods we explicated or others developed by independent researchers) will lend greater support to the hypothesis that anthropogenic impacts account for decreasing mussel size distributions in archaeological contexts.

2. Conclusion

We contend that full and detailed appreciation of nuanced human interactions with the environment is important, relevant, and informative. Archaeologists should not ignore ecological data at any scale. It is impossible to fully understand the complexity of a forest (let alone human interactions with the forest) without first studying the trees, and shrubs, and flowers, and fungi, and insects, and so on. Ecological interactions can only be understood by carefully studying the component parts, as well as how they interact and pull on each other. Without a clear and detailed understanding of this deep web of interconnectedness we can have no true understanding of the forest, or the trees. If we archaeologists want to understand the adaptations or impacts of ancient coastal foragers, we must assiduously seek to better understand the nuance, details, and small-scale variability (both spatial and temporal) in resource distribution, abundance, and quality.

As global efforts to understand and document anthropogenic impacts on the environment recently have increased dramatically, so have archaeologists' eagerness to contribute relevant research. Archaeological materials (both *in situ* and in repositories) undoubtedly can contribute immensely to these efforts as “distributed observing networks of the past” (“DONOP”-*sensu* IHOPE, 2016). However, as scientists and scholars, we must remain vigilant regarding the appropriate use and interpretation of archaeological data; especially in the context of interdisciplinary research agendas.

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