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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., 2016) 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 (2016) 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., 2016). 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 overarching 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. 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. 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 (2016) 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