Reconsidering evidence of human impacts: Implications of within-site variation of growth rates in *Mytilus californianus* along tidal gradients

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ABSTRACT

Disentangling the complex web of human and natural effects that structure archaeological shellfish assemblages remains a challenging process that requires careful consideration of interdisciplinary datasets. The ecological data presented in this paper demonstrate highly variable growth rates within intertidal patches of *Mytilus californianus*. These results fill a spatial and conceptual gap in our understanding of small-scale variability in mussel growth rates and terminal shell size, and have significant implications for understanding ancient human foraging behavior, as well as how we interpret archaeological signatures of anthropogenic impact on mussel populations. We evaluate how small-scale variation along tidal gradients structures the size of resources available to coastal foragers throughout the lunar cycle. This ecological study leads us to propose that increased exploitation of smaller mussels available at higher shore levels during less favorable tides could result in archaeological assemblages that mimic the expected correlates for resource depression, thus, confounding interpretation of human impacts.

1. Introduction

Archaeological evaluation of human impacts on shellfish populations commonly relies on proxy measures for resource depression, including decreasing shell size and increasing diet breadth, among others (see Mannino and Thomas, 2002 for a comprehensive review of this subject). In California, many archaeological studies highlight a diminution in size of *Mytilus californianus* (California mussel) as evidence of increased predation pressure and reduced foraging returns (Botkin, 1980; Braje et al., 2007; Erlandson et al., 2008; Glassow et al., 2008; Erlandson et al., 2011; Braje et al., 2012). In these studies, intertidal resources are invariably characterized as "especially vulnerable to human predation because most are sessile, predictable, and require little specialized technology to exploit" (Erlandson et al., 2008:2145). Researchers argue that resource depression occurs due to recurrent extraction of large individuals, which decreases the probability of survival with age and effectively reduces the average age and size of the natural shellfish population (Whitaker, 2008:1115). Data from modern ecological research substantiates this proposed relationship, documenting

cases in which increasing human harvesting affected the growth rate, size, and abundance of targeted species as well as non-harvested species (Castilla and Duran, 1985; Lasiak and Field, 1995; Sagarin et al., 2007). However, ecological research also indicates mussel size and abundance are mediated by a wide array of environmental factors operating variably at regional, local, and within-site scales.

Disentangling the confounding effects and interactions of both environmental and anthropogenic influences is a challenging process that requires interdisciplinary approaches. In this paper, we present data from a recent ecological experiment designed to evaluate variation in growth rates of *Mytilus californianus* at two distinct micro-geographic scales: (1) local, between sites across the island landscape and (2) within-site across an individual intertidal patch. We argue that consideration of small-scale, particularly within-site variability—as this is the level at which human foragers interact with intertidal populations—has significant implications for interpreting shellfish harvesting decisions and evaluating potential human impacts.

1.1. Cultural context of mussel exploitation

The archaeological record from California's Northern Channel Islands documents over 13,000 years of human exploitation of the

nearshore and intertidal marine environment. With restricted terrestrial resources available throughout the Holocene, early is- land residents relied heavily on easily accessible intertidal and nearshore marine habitats for dietary protein contributions (Erlandson, 1984, 1988, 1991; Erlandson et al., 2008). Molluscan populations provided an important staple resource in the Island Chumash subsistence economy throughout prehistory (Erlandson, 1988; Glassow, 1993; Kennett, 2005). This fact is acutely demon- strated by the prevalence of extensive shell middens across the islands, which are the byproduct of prehistoric dependence on intertidal shellfish species for subsistence (Glassow, 1993; Kennett et al., 2007). The majority of the recorded archaeological shell middens are most commonly composed of a high density of Cali- fornia mussel shell.

For example, Flores Fernandez (2014:62) recently found that the relative proportion of mussel shells recovered from two diachronic archaeological assemblages was roughly double the proportion of mussels occurring in modern intertidal mussel beds around Santa Cruz Island, providing clear evidence of intensive reliance on this key resource. As the potential for human predation to significantly impact intertidal resources is dependent on the relative economic importance of prey species (Mannino and Thomas, 2002), it is appropriate that various research projects on the Northern Channel Islands focused on the potential impacts of long-term intensive human foraging (see for example Erlandson et al., 2005; Rick et al., 2006; Braje et al., 2007, 2008, 2012; Kennett et al., 2007; Rick and Erlandson, 2009).

Based, in part, on these studies, archaeologists argue that during the Late Holocene (3000–200 cal BP) human population levels increased, leading to habitat infilling and territorial circumscription on the three largest of the Northern Channel Islands (Winterhalder et al., 2010:10). This period is defined by critical shifts in the forager economy as relatively egalitarian hunter–gatherers, once heavily focused on shellfish and terrestrial plant foods, became socially complex maritime chiefdoms, intensively exploiting nearshore and pelagic fisheries (Winterhalder et al., 2010:16). Major Late Holocene village settlements, documented by the presence of laterally extensive and deep shell midden deposits, tethered the prehistoric Chumash to coastal locations throughout the year (Kennett, 2005). Winterhalder et al. (2010:10) note that these settlement locations provided island foragers with immediate access to and control over productive (and critical) nearshore and intertidal marine resources. Within this broader cultural context, researchers assert that, as preferred habitats on the Northern Channel Islands became satu- rated, human predation pressure contributed to declines in envi- ronmental suitability (e.g., Kennett et al., 2009). Thus, Braje et al. (2012:118) suggest that the deleterious effects of foraging pres- sure structured shellfish harvesting decisions, resulting in pro- gressive decreases in the mean size of California mussel collected and increase in the overall diversity of shellfish taxa collected.

1.2. Ecological context of mussel exploitation

Effective argument that shell size decrease represents resource depression must critically evaluate, or control for, the full range of environmental influences on mussel growth rates. Growth in *Mytilus californianus* is indeterminate. The growth rate and body size at any age are predominantly determined by a complex mosaic of environmental and ecological factors that influence physiological trade-offs between growth and survival (Connor and Robles, 2015:40). Intraspecific competition often results in dense mussel beds dominated by larger individuals that monopolize space on the rocks crowding out smaller individuals (Botkin, 1980; Blanchette and Gaines, 2007:277). Although reduced growth rates have been documented in dense mussel beds, the removal of larger

individuals (by human and non-human predators) may relieve intraspecific competition within beds enhancing the growth rate of the remaining mussels (Yamada and Peters, 1988:298). Moreover, prior large-scale studies found that regional differences in the concentration of phytoplankton contribute to regional-scale spatial differences in mussel growth (Menge, 1992; Menge et al., 1994), as does seasonal upwelling (Blanchette et al., 2005, 2006) and sea surface temperature (Blanchette and Gaines, 2007). Another regional-scale comparison (Blanchette and Gaines, 2007) found a negative correlation between wave exposure and growth in Cali- fornia mussels. However, the results of this study indicated that the influence of wave exposure was confounded by shore-level differ- ences that affect submergence and feeding times. This provocative finding highlights the potential significance of within-site location as a critical environmental constraint on mussel growth. As dis- cussed in Flores Fernandez (2014:18–19), environmental factors that contribute to macro-scale regional variation in mussel distri- bution, abundance, and size, can also exert significant small-scale variation that can exceed regional-scale variation. Indeed, within any given intertidal patch, microhabitat sea surface temperature (SST), tide level, and wave action modify levels of feeding oppor- tunities and thermal stress that mussels experience—all of which exert significant influence on the growth rates of individual mus- sels (Helmuth, 1999; Helmuth and Denny, 2003; Helmuth et al., 2006).

Recent ecological studies call for increased attention to these physical parameters and organism responses at the fine scales at which they experience it—that is, meters within a given intertidal patch (Connor and Robles, 2015:39). We believe that a similar call also must be made in archaeological evaluation of mussel size, which may reflect growth rates that vary over meters within the intertidal environment. Although many researchers attempt to control for large regional scale variation in mussel growth rates based on these environmental factors, the tenuous underlying assumption persists that shellfish growth rates are constant within intertidal patches. Controlling for regional factors alone does not adequately control for local, between site (across the island land- scape) or within-site (across an individual intertidal patch) varia- bility—and this, of course, is the scale at which human foragers interact with the intertidal community and California mussel populations.

To address these issues we assess how small-scale, local and within-site variability affects the growth of *Mytilus californianus* between and within two discrete intertidal patches on Santa Cruz Island. We hypothesized that the tidal gradients in temperature, wave exposure, submersion, and areal exposure would exert in- fluences on growth rates of mussels, potentially underlying small- scale differences in the mean size of individuals within each pop- ulation. This study provides a quantitative assessment of mussel growth rates across the tidal gradient. This ecological study leads us to propose that increased exploitation of smaller mussels available at higher shore levels during less favorable tides could result in archaeological assemblages that mimic the expected correlates for resource depression, thus, confounding interpretation of human impacts.

2. Regional setting

The Northern Channel Islands and surrounding waters contain an incredibly diverse assemblage of marine species (Murray and Littler, 1981). This diversity is largely attributable to exposure to varying oceanographic conditions, high productivity resulting from upwelling of cold nutrient-rich water, and the diversity of habitat types (Blanchette et al., 2008:162). Oceanographic conditions mediate the structure of nearshore biological communities via

delivery of nutrients and larvae and influences on growth, productivity, and reproduction (Blanchette et al., 2008:162). The Santa Barbara Channel is influenced by two major current systems, the cold southward flowing California Current, and the warm westward flowing, nearshore southern California Countercurrent (Hickey et al., 2003). This variability results in a persistent thermal gradient along the channel, with higher sea surface temperatures (SST) in the southeastern portion associated with the influx of warmer subtropical water and the topographic deflection of equatorward, upwelling-favorable winds at Point Conception in the northwestern opening of the channel (Hickey, 1992; Winant et al., 2003; Otero and Siegel, 2004). In contrast, the northwestern part of the Southern California Bight experiences much colder conditions because of the intense advection of cold water from the nearby Point Conception and Point Arguello upwelling centers (Hickey, 1992; Winant et al., 1999, 2003). The influence of this cold California Current, coupled with seasonal upwelling, provides the foundation for high marine productivity and the rich intertidal biodiversity in the region (Kennett, 2005:55).

Santa Cruz Island, the largest, most ecologically and topographically diverse of the four Northern Channel Islands, is situated 35 km off the California coast directly within the confluence of these two major current systems (Broitman et al., 2005:1474). The irregular geomorphology of the island's shoreline incorporates rocky headlands and intertidal zones, sandy beaches, coves, and low sloping marine terraces (Glassow, 1997; Kennett, 2005). The distribution and characteristics of these habitats vary greatly across the island landscape. Much of the northern shore is rugged, with plunging cliffs interspersed by small pocket beaches at canyon mouths; discrete stretches of sandy beach appear along portions of the western and southern shores complemented by the shallow rocky reefs that dominate most of the shoreline (Hewitt, 1946:189; Glassow, 1997; Kinlan et al., 2005:131). Although, molluscan resources are densely distributed around the whole perimeter of the island, these communities exhibit a great deal of small-scale ecological and oceanographic variability (e.g., Broitman et al.,

2005; Blanchette, et al., 2006, 2009) that most certainly had important implications for ancient human foraging on *Mytilus californianus* beds (see for example Flores Fernandez, 2014).

3. Material and methods

3.1. Study sites

Over the course of an eleven-month study, we conducted mussel growth experiments at two intertidal locations with extant mussel beds near known archaeological dense shell midden deposits (Fig. 1). One site was located on the northwest shore of the island (Fraser Cove) and the other on the southeastern shore (Willows). These locations are both gently sloping (0–20°) rocky benches, selected to be as similar as possible in terms of geomorphology, wave exposure, and habitat type (see Blanchette et al., 2008 for more detail). Both sites were characterized by midintertidal zones dominated by *Mytilus californianus* as well as other flora and fauna characteristic of wave-exposed rocky shores. Steep cliffs and sandy beaches dominate much of the coast between the two study sites. A persistent gradient in sea surface temperature (SST) exists between western and eastern ends of the island (Blanchette et al., 2006), results in consistently cooler local SST regimes at Fraser Cove than at Willows. We expect this persistent difference in SST between these two sites to result in significantly different mussel growth rates between the two sites. These two locations were chosen based on accessibility and to be generally representative of the intertidal flora and fauna of that island region. Additionally, both locations are long-term ecological monitoring sites with ongoing data collection efforts led by major research groups.

3.2. Experiment design

To quantify growth rates of mussels, we collected 160 small (3–5 cm), similarly sized *Mytilus californianus* from each study site
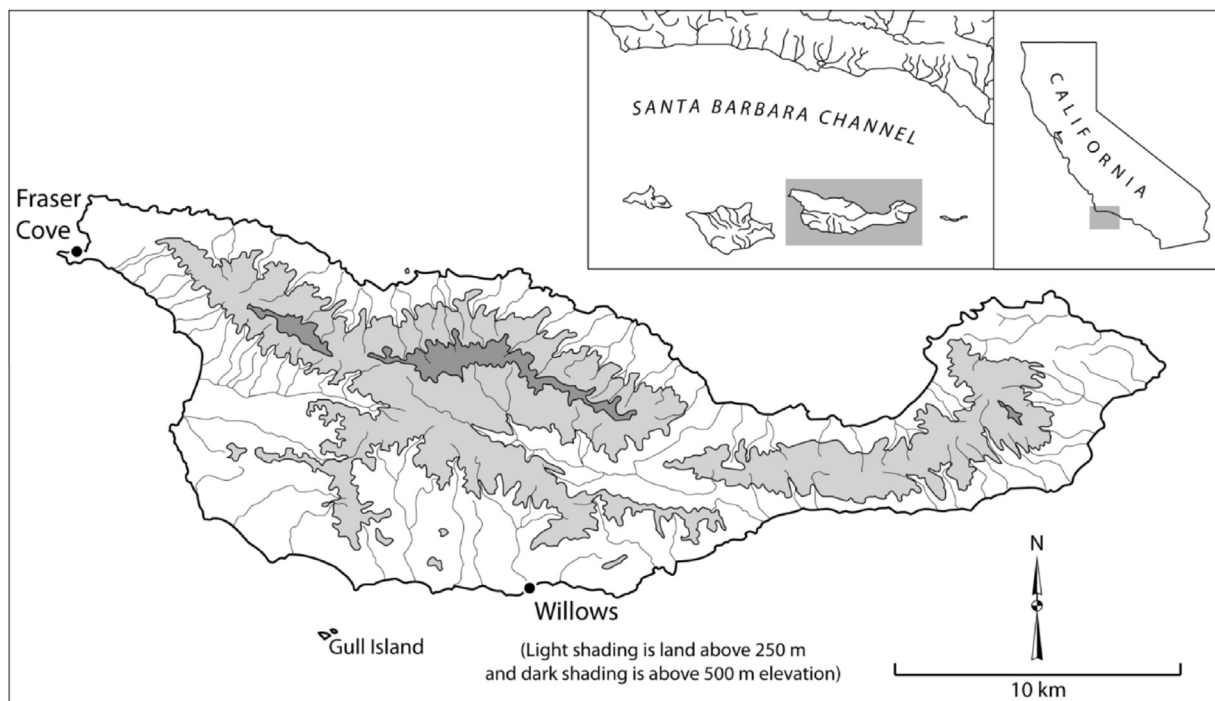

Fig. 1. Location of study sites on Santa Cruz Island, CA.

Fig. 2. Example of mussel shell from lowermost experimental plot at Willows with key characteristics measured for growth calculations.

the new shell edge. Marked mussels were recovered and collected after eleven months (February 2013–January 2014) and brought to the laboratory. The shell length (i.e., the anatomical height) of the mussels was measured to the nearest 0.1 mm with Vernier calipers from the umbo to the initial ventral margin (marked by the notch) and from the umbo to the final ventral margin of the shell. The distance from the umbo to the notched initial ventral margin represents the initial length at the time when the mussels were translocated. The second measurement from the umbo to the final ventral margin of the shell incorporates the increment of shell growth that occurred during time of deployment (see Fig. 2). To compare growth within sites and across tidal gradients, we calculated size specific growth rates as the change in shell length divided by the final mussel length and the total number of days in the experiment (*sensu* Blanchette et al., 2006). We also consider differences in local site-specific mussel growth rates.

3.3. Statistical analysis

All analyses were performed with SYSTAT statistical software (v9). We examined probability plots of residuals for the assumption of normality, and plots of residuals vs. estimated values for independence of error terms. Data not meeting these assumptions were appropriately transformed. We analyzed mussel growth using a one-way ANOVA and performed post-hoc Tukey HSD tests to evaluate the statistical significance of differences among plots at each site. We used a pooled t-test to evaluate the statistical significance of differences between the two study sites.

4. Results

At Fraser Cove a total of 95 mussels survived the eleven-month (340-day) study in the transplanted plots, as compared to Willows where just 54 mussels survived in the transplanted plots. The much greater mortality evident at Willows appeared related to vandalism. The plastic mesh cages of the upper two plots were damaged leading to the complete loss of mussels transplanted to W-1 in the splash zone and all but nine individuals (22.5%) in W-2 in the emersion zone. By comparison 28 individuals (70%) survived in FC-1 in the splash zone and 20 individuals (50%) in FC-2 in the emersion zone at Fraser Cove. Descriptive statistics summarizing mussel survivorship, growth, and growth rates for each plot at Fraser Cove and Willows are presented in Table 1.

and translocated them into four plots aligned vertically across the tidal gradient at each site using methods described in detail in Menge et al. (1997) and Phillips (2005). One plot was established in the lowest accessible portion of the rocky bench (during minus tides) in the full immersion zone of the subtidal, two plots were established in the emersion zone of the lower and middle intertidal, and one plot was established in the splash zone of the upper intertidal. The plots were labeled 1 to 4, from shallow to deep, with the prefix FC for Fraser Cove and W for Willows. Thus, the highest plot at Willows is designated as W-1 and the lowest plot is W-4. We marked mussels by filing a small (~1 mm) triangular notch on the posterior shell edge of each mussel without disturbing the soft tissue. The four groups of 40 mussels (selected at random from the population of 160) were placed ventral side down in their natural position and covered with plastic mesh cages to allow them to reattach to the rock with their byssal threads. We observed in earlier experiments that few byssal threads are produced if the

Table 1
Descriptive statistics summarizing mussel survivorship, growth, and growth rates for each plot at Fraser Cove and Willows.

Site/Plot	ID	N	Min growth (mm)	Max growth (mm)	Median growth rate	Mean growth rate
Fraser Cove, Uppermost Plot	FC-1	28	0.0	3.8	0.00	3.26
Fraser Cove, Mid-intertidal Plot	FC-2	20	0.0	3.3	8.33	11.73
Fraser Cove, Lower-intertidal Plot	FC-3	23	3.7	11.4	48.20	48.83
Fraser Cove, Subtidal Plot	FC-4	24	4.9	20.2	79.86	79.74
Willows, Uppermost Plot	W-1	0	–	–	–	–
Willows, Mid-intertidal Plot	W-2	9	5.1	12.8	59.29	51.29
Willows, Lower-intertidal Plot	W-3	15	5.2	26.6	110.96	100.80
Willows, Subtidal Plot	W-4	30	3.4	26.6	71.60	72.64

cages remain snug, so to encourage the more rapid production of threads, we loosened the cages (i.e., increased the space between the mussels and the mesh) after six weeks (April 2013).

Mussel growth was estimated as the shell material added since translocation, quantified as the increment between the notch and

4.1. Local variation between sites

Growth rates from the two lower transplanted plots, one in the lowest accessible portion of the rocky bench (during minus tides) and one from the lower intertidal, at each site were assessed to

evaluate local variation between the two locations. Although data from FC-1 and FC-2 at Fraser Cove were available, these data were omitted to compensate for the lack of comparable data from the W-1 and W-2 at Willows. Results of the t-test confirmed significant difference in mussel growth rates from FC-3 and FC-4 at Fraser Cove (Mean = 64.61, SD = 21.28) and from W-3 and W-4 at Willows (Mean = 82.00, SD = 31.45), $t(92) = -3.119$, p = 0.002). In agreement with previous ecological research (see Blanchette et al., 2006), California mussel growth rates are significantly higher at Willows than they are at Fraser Cove, demonstrating significant local variation likely due to the effects of dynamic oceanographic patterns that expose these two locations to different mean SSTs (see Flores Fernandez (2014) and Glassow et al. (2012) for discussion).

4.2. Within-site variation across the tidal gradient

Our results document the existence of a steep gradient in mussel growth rates related to tidal elevation within each site. Results of the one-way ANOVA used to evaluate differences between transplanted plots within each site indicate that low-zone mussels experience significantly higher growth rates than mid-zone and upper-zone mussels exposed to similar site conditions (seawater temperature, food, wave exposure, etc.).

At Fraser Cove mussel growth rates varied widely, resulting in a maximum of 20.2 mm and a minimum of 0.0 mm shell growth over the eleven-month study. The growth rate estimated for all mussels differed significantly between the four tidal gradient plots ($F(3,74) = 78.622$, d.f. = 3, p = 0.000). Tukey post-hoc comparisons of the four transplanted plots (FC-1, FC-2, FC-3, FC-4) indicate that mean growth rate of mussels in the subtidal plot was significantly higher (Mean = 79.74), than the mean growth rate of the lower intertidal plot (Mean = 48.83, p = 0.000), the middle intertidal plot (Mean = 11.73, p = 0.007), and the upper intertidal (Mean = 3.26, p = 0.000). In contrast, comparisons between the upper intertidal and middle intertidal plots demonstrate no significant difference in growth rate (p = 0.957). However, it is worth noting that only eight of the 28 surviving mussels (28.5%) from the upper intertidal plot exhibited any observable growth at all. All other comparisons between plots were significant (p = 0.000) and support the interpretation that growth rates increase progressively with tidal elevation (Table 2).

Table 2
Results of ANOVA among plots on mussel growth rates at Fraser Cove.

Source of variation	df	SS	MS	F	p
Plot	3	63.715	21.238	78.622	0.000
Error	70	18.909	0.270		

Similar to Fraser Cove, at Willows mussel growth rates also varied widely, resulting in a maximum of 26.6 mm and a minimum of 3.4 mm shell growth over the eleven-month study. The growth rate estimated for all mussels differed significantly between the three lower tidal gradient plots ($F(2,51) = 10.083$, d.f. = 2, p = 0.000). Tukey post-hoc comparisons of these three plots (W-2, W-3, W-4) indicate that mean growth rate of mussels in the lower intertidal plot (Mean = 100.80) was significantly higher than the mean growth rate of the subtidal plot (Mean = 72.64, p = 0.006) as well as the middle intertidal plot (Mean = 51.29, p = 0.000). In contrast, the higher mean growth rate for mussels from the subtidal plot in comparison to the middle intertidal plot is only marginally

significant (p = 0.135) (Table 3). This final comparison may be affected by the small sample size from the middle intertidal plot (Table 1).

Table 3
Results of ANOVA among plots on mussel growth rates at Willows.

Source of variation	df	SS	MS	F	p
Plot	2	15028.017	7514.008	10.083	0.000
Error	51	38004.843	745.193		

At both sites, there is evidence of a relationship between mussel growth rate and tidal elevation. Due to highly variable growth rates, size zonation is apparent, with larger, faster growing mussels most abundant in the lower reaches of the rocky bench and smaller, slower growing mussels most abundant in the upper portions of the intertidal. Although growth is greatest at sites where the tidal elevation of mussel growth plots is lowest, there may not be a simple relationship between tidal elevation and submersion time, particularly if shifts in tidal elevation are related to variation in wave exposure, and both are likely to have independently strong influences on growth (see Connor and Robles, 2015).

5. Discussion

Our results document significant variation in growth rates of *Mytilus californianus* at two distinct micro-geographic scales: (1) local (between sites) and (2) within-site. This research supports previous evidence of differences in mussel growth rates between Willows and Fraser Cove, demonstrating significant local variation (see Blanchette et al., 2006). Furthermore, this research confirms significantly increased California mussel growth rates toward lower tidal elevations of rocky intertidal patches at both sites, demonstrating significant within-site variation. Although we did not directly test the possible mechanisms (e.g., water temperature, food quality and quantity, and wave exposure, among others) driving differential growth rates across the tidal gradient, it is clear that such environmental conditions influence the relative size of mussels across comparatively small spatial scales. These results contribute to a greater understanding of small-scale variability in mussel growth rates and terminal shell size, which has significant implications for understanding ancient human foraging behavior, as well as how we interpret archaeological signatures of anthropogenic impact on mussel populations. In the following discussion we evaluate factors that likely contribute to variable mussel growth rates, consider how small-scale variation structures the resources available to coastal foragers throughout the lunar cycle, and lastly, propose an alternative hypothesis for understanding archaeological patterns commonly attributed to human impacts.

5.1. Understanding small-scale variation

Much is known about the physiology and ecology of the genus *Mytilus* (see review by Zippay and Helmuth, 2012:315). Macro-scale variation in California mussel growth rates is well established in the ecological literature and widely recognized by archaeologists. The same environmental factors (see preceding discussion) that drive regional variation in mussel distribution, abundance, and size can also exert significant small-scale variation at the local and within-site level. Therefore, it is essential for archaeologists to understand, and critically evaluate, the full range of environmental influences across the island(s) and within the intertidal landscape. In this section, we focus specifically on within-site variation, as Flores Fernandez (2016), also included in this special issue on

archaeomalacological methods, evaluates evidence of small-scale variability at the local level on Santa Cruz Island. Considering both ecological and archaeological datasets, she argues that controlling for regional factors alone does not adequately control for local variability in the size and abundance of California mussel in beds located patchily around the island perimeter (Flores Fernandez, 2016). We refer the reader to this companion article for an in-depth discussion regarding the potential muddling effects of local variability in mussel growth rates on the interpretation of ancient human impacts on California mussel.

Recent ecological studies, including the work presented in this paper (see also Fitzgerald-Dehoog et al., 2012; Connor and Robles, 2015), go even further, assessing within-site variation of growth rates and terminal sizes in *Mytilus californianus* along tidal and wave-exposure gradients. Unlike mobile animal populations, which can simply move to more favorable microenvironments, sessile mussels are significantly impacted by this variation resulting in physiological trade-offs between growth and survival similar to those documented at much larger spatial scales (Blanchette and Gaines, 2007). Previous studies document that mussel growth rates increase with a decrease in emersion time (Seed, 1968; Griffiths, 1981; Rodhouse et al., 1986) and that subtidal mussels grow at faster rates than intertidal mussels (Yamada and Peters, 1988; Yamada and Dunham, 1989), as indeed we find in this experimental study.

Researchers hypothesize that slower growth among animals higher in the intertidal zone may occur due to the relatively greater amount of time spent undergoing aerial respiration, due to increases in the amount of energy allocated to stress responses, or both (Dittman and Robles, 1991; Hofmann and Somero, 1995; Roberts et al., 1997; Somero, 2002). Additional ecological studies demonstrate that the largest mussels tend to be prevalent in the lowest intertidal, and sizes tend to decrease going up the shore (Paine, 1974; Suchanek, 1992; Marsden and Weatherhead, 1999). Our results reinforce these general findings and provide a quantitative demonstration that individuals lower on the shore have significantly higher growth rates than those higher on the shore resulting in zonation based on size, but not necessarily ontogenetic age. Given this, it is necessary to consider carefully the use of size as a proxy for human impacts on California mussel (Botkin, 1980; Braje et al., 2007; Erlandson et al., 2008; Glassow et al., 2008; Erlandson et al., 2011; Braje et al., 2012).

5.2. Implications for human foraging behavior

Archaeologists working on the Northern Channel Islands often assert that low tides facilitated daily access to and human predation on mussel beds in the highly productive littoral environment that surrounds the Northern Channel Islands (Braje et al., 2007:739; Erlandson et al., 2008:2145). While this is true, it is also important to recognize that not all tides are equal. The coast of Southern California experiences a mixed semidiurnal tidal regime, in which two unequal high tides alternate with two unequal low tides each lunar day. Maximum tidal amplitudes (spring tides) occur every 14.5 days in a lunar cycle, coincident with the new and full moon. Seasonal tidal patterns, particularly the occurrence of diurnal tides, exert significant influence on human foraging by mediating daytime access to the lower reaches of mussel beds where larger, faster-growing individuals are available. In the Santa Barbara Channel Region, the lowest tides occur during winter and summer months—coincident with the winter and summer solstice—with tides of lower amplitude in spring and fall. The lowest fall-through-winter tides occur in the afternoon, whereas the highest tides occur in the morning. In spring-through-summer, the lowest tides occur in the morning, while the highest tides occur at night (Goleta

Slough Management Committee, 2015; NOAA, 2015). Ecologists engaged in long-term monitoring of intertidal resources across Santa Cruz Island preferentially schedule research excursions to coincide with favorable diurnal low tides during the winter. The prehistoric inhabitants of Santa Cruz Island were certainly aware of tidal movements, and it is reasonable to expect that they adjusted their foraging behavior to maximize returns.

Ethnographic studies from around the world document the influence of tidal regime on human exploitation of intertidal resources. Modern and historic coastal foragers indicate a strong preference for shellfish collection during high amplitude diurnal spring tides that expose the full extent of the intertidal shore (Kingsford et al., 1991; Lasiak, 1997; Bird and Bliege Bird, 2000; Bleige Bird and Bird, 2002; De Boer et al., 2002; Rius and Cabral, 2004; Aswani et al., 2015; Thomas, 2014). Some ethnographic cases, such as Jimenez et al. (2011), indicate negligible shellfish harvesting outside of the daytime spring tides; others document increased harvesting in the upper portions of the intertidal zone during low amplitude neap tides (roughly every 14 days) and seasonally nocturnal low tides. As discussed by Thomas (2014:208), tidal movements act as constraints on decisions to continue harvesting in a high-ranking patch and face diminishing returns, because of increasing difficulty associated with the incoming tide, or to move to a less productive patch at higher shore-level. Bird et al. (2004:9) also indicate that coastal foragers choose to exploit lower ranked patches at higher shore-level when the mid-littoral is not fully exposed by daytime tide. In other words, although shellfish collection throughout the intertidal zone is possible (via wading or even diving) without low diurnal tides, which expose larger, faster growing mussels, it may be significantly more costly (and riskier, in the case of diving along rocky wave-exposed shorelines) than simply harvesting smaller, slower-growing mussels at a higher shore-levels. Moreover, children, prone to forage on safer higher shore-levels, also contribute to daily catches and introduce additional variability (Bird and Bliege Bird, 2000).

Tidal variation introduces predictable short-term spatial and temporal constraints on mussel exploitation. For at least two weeks every month, during neap tides, and perhaps longer during seasons in which low tide occurs outside of daylight hours, the ancient inhabitants of Santa Cruz Island experienced decreased access to (or increased costs associated with accessing) the lower reaches of the intertidal zone. If the prehistoric inhabitants of the Northern Channel Islands did indeed rely on daily access to mussel beds throughout the lunar cycle, then we should expect to see variation in the array, abundance, and size of shellfish collected. The diet breadth model predicts that foragers seeking to maximize return-rates in a rich (spring tide) environment should focus on only the most profitable species, such as larger, faster growing mussels; whereas, in a poor (neap tide) environment diet should be broader, including an array of less profitable taxa, such as smaller, slower growing mussels (De Boer et al., 2002:239). Among traditional coastal foragers in South Mozambique, De Boer et al. (2002) document significant variation in mean neap tide and spring tide catches, reflecting differential foraging strategies practiced in response to the relative exposure of the intertidal. During spring tides when larger areas were exposed, catches included significantly fewer, but significantly larger shellfish. In contrast, during neap tides when less area was exposed, catches included significantly more, but significantly smaller shellfish accompanied by a higher diet breadth (De Boer et al., 2002). This harvest pattern is consistent with our local expectations for neap tide catches based on within-site variation in mussel growth rates and diet breadth models derived from optimal foraging models. Higher-shore neap tide catches on Santa Cruz Island should include, on average,

smaller (but not necessarily younger) California mussels. Decreased mussel return rates should favor inclusion of lower ranked taxa effectively expanding diet breadth.

Nonetheless, the preceding discussion hinges on the assumption that ancient foragers relied on regular, perhaps even daily, exploitation of intertidal mussel beds; yet this is not actually known to be true for prehistoric samples. In the ethnographic examples discussed above, some foragers eschew intertidal resources altogether during less favorable tidal patterns (see Jimenez et al., 2011). Central place foraging models, also derived from optimal foraging theory, predict that resource scheduling reflects not only the predictability, patchiness, and distribution of the resource, but also the relative degree of population mobility (Grayson and Cannon, 1999). We expect that highly mobile foraging peoples mapped onto intertidal patches during the period of highest potential return rate. In other words, prior to evidence of increasing circumscription and coastal sedentism, we expect that the prehistoric inhabitants of Santa Cruz Island scheduled exploitation of mussel beds to coincide with favorable diurnal spring tides when the largest area of the intertidal zone was exposed. In contrast, we expect that large sedentary populations experiencing increasing circumscription more readily exploited resources during periods of lower return rates. This is due, in part, to decreased foraging radii. The relative cost associated with exploiting mussel beds within immediate proximity of large coastal villages was most certainly lower than the relative costs of exploiting the same mussel beds via logistical forays from residential bases located elsewhere on the island landscape. Once tethered to large coastal villages, the prehistoric inhabitants of Santa Cruz Island may have been more willing to accept lower return rates associated with exploitation of the upper shores during monthly neap tides and seasonally nocturnal low tides. Thus, we argue that daily exploitation of mussel beds throughout the lunar cycle most probably co-occurs with increasing sedentism and that the resultant shellfish assemblage should mirror local expectations for neap tide catches.

5.3. Reconsidering evidence of human impacts

The potential for human foragers to impact shellfish resources is widely accepted (Thomas, 2015:161); however, a decrease in mean shell size over time in archaeological deposits should only be attributed to anthropogenic impacts if and when environmental causes can be controlled for or discounted (Giovas et al., 2013). Researchers are increasingly aware of complex interactions between life history variables unique to target species and environmental factors that confound evidence of harvesting pressure (Grayson and Cannon, 1999; Claassen, 1999; Broughton, 2002; Mannino and Thomas, 2002; Giovas et al., 2010, 2013; Thakar, 2011). In the case of California mussel, archaeologists are generally careful to provide in depth discussion of ecology, taking into account broad regional and temporal variation in SST and marine productivity, which are known to influence mussel abundance, distribution, and size. Nonetheless, evidence of decrease in average size of California mussel is now almost routinely attributed to resource depression and anthropogenic impacts (Braje et al., 2007; Erlandson et al., 2008; Glassow et al., 2008; Erlandson et al., 2011; Braje et al., 2012). Discussions of shellfish foraging behavior on the Northern Channel Islands overlook the influence of small-scale variation in mussel growth rates within a given intertidal patch as well as the resulting pattern of size gradation (unrelated to age). These factors significantly alter the size of mussels available to neap tide collectors versus spring tide collectors. Increased exploitation of smaller mussels and other taxa readily available at higher shore levels during less favorable tides could result in archaeological assemblages that mimic the expected correlates for resource

depression. Therefore, an alternative hypothesis presents itself: Increasing circumscription and coastal sedentism required more regular, even daily, shellfish exploitation and concomitant increased reliance on neap tide foraging. This hypothesis would readily explain decreased average size in California mussels in the absence of resource depression or any demonstrable human impact.

5.4. Potential methods for evaluating tidal signature in the archaeological record

Whether this hypothesis is supportable must be evaluated through reference to the archaeological record. Despite significant differences in the fine grained time-scales represented by this ecological study and the coarser grained time-scales represented by the archaeological record, methods for discerning the potential role of tidal patterns in structuring archaeological shellfish assemblages emerge from recent archaeomalacological studies. Although there is no single pattern associated with tidal regime, researchers effectively argue that changing frequencies of mollusc species available at different heights in the intertidal zone provide a proxy measure for identifying potential tidal signatures. Jerardino (2014) finds that the relative abundance of specific low-intertidal/subtidal limpets co-varies with the occurrence of large edible barnacles and modest surges in mussel shell size. Based on this evidence she argues that shellfish collection most probably occurred during exceptionally low spring tides when these particular resources would have been more accessible to human foragers. Seasonality studies that indicate spring and autumn coastal site visitation, coincident with equinoctial-spring tides, bolster this argument (Jerardino, 2014:61). Similarly, Langejans et al. (2012) argue that low-tide intertidal foraging corresponds with greater representation of high-ranked, low-living species in the archaeological assemblages.

Another promising method relies on oxygen isotope analysis to evaluate differences between the inferred SSTs that different species, recovered from the same stratigraphic context, were living in at the time of harvest. Rick et al. (2006) demonstrate exploitation of subtidal patches based on the contemporaneous harvest of abalone from colder waters and California mussels from warmer waters at the same location. Although Rick et al. (2006) do not argue that harvest strategy is related to low spring tide collection, it stands to reason that this method could be easily adapted to test within-site temperature variation, which logically corresponds to intertidal elevation. Another approach relying on oxygen isotope analysis is suggested by Glassow et al. (2012). In this research, carbonate samples collected at regular intervals along the primary growth axis of some mussel shells demonstrate more rapid increases and decreases in SST than samples collected at similar intervals from other shells. The authors suggest that this "saw-tooth" pattern, in contrast to a more sinusoidal pattern, results from more rapid growth. Therefore, the proportion of faster growing relative to slower growing mussels, could be assessed using a well-designed program of oxygen isotope analysis that demonstrates the relative frequency of faster verses slower growth rates. These methods provide tangible means of evaluating the potential role of tidal patterns in structuring archaeological shellfish assemblages and discerning whether shell size variation is an artifact of higher-shore foraging.

6. Conclusions

Disentangling the complex web of human and natural effects that structure archaeological shellfish assemblages remains an evolving process that requires careful and detailed consideration of

many diverse datasets. The ecological data presented in this paper fill a spatial and conceptual gap in our understanding of small-scale variability in *Mytilus californianus* growth rates. Discussion of within-site size zonation across the tidal gradient demonstrates the importance of small-scale variability in structuring the average size of California mussel available to human foragers during neap tides and nocturnal low tides. We propose that archaeological evidence of diminution of mussel shells and concurrent increases in the number of intertidal taxa exploited may correspond to expectations for higher-shore foraging during monthly neap tides, seasonal nocturnal low tides, or both. This has important implications for how archaeologists interpret evidence of prehistoric human impacts on California mussels. The archaeological correlates for higher-shore foraging mimic the commonly accepted archaeological correlates for resource depression and confound such interpretations.

We do not suggest that archaeologists should abandon consideration of human impacts on California mussel or that these two explanatory models are mutually exclusive. However, we do assert that multiple lines of evidence and multiple working hypotheses are necessary to evaluate fully the relative importance of anthropogenic versus environmental influences structuring archaeological shellfish assemblages. We agree with Jerardino (2014:61) that engaging more fully with ecological variables will serve to maximize and strengthen interpretations based on the archaeological record. Although this paper specifically addresses California mussel on Santa Cruz Island, small-scale variability in intertidal ecology is not unique to this species or to this geographic region. Rather, "it is an intrinsic characteristic of coastal environments around the Atlantic, the Pacific and other oceans. Small-scale variation influenced coastal foraging behavior through the course of prehistory, and therefore it has to be studied and included in any research that aims to understand human-coastal environmental interactions and marine resource use in the past anywhere around the world" (Flores Fernandez, 2014:86). Moreover, this research contributes to a broad zooarchaeological efforts (e.g. Whitaker, 2009; Wolverton et al., 2012) to develop better understanding of individual and population growth dynamics of harvested species in relationship to the environment, so that we might reach more reliable interpretations of archaeological evidence about subsistence.

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