



Making the most of fragments: a method for estimating shell length from fragmentary mussels (*Mytilus californianus* and *Mytilus trossulus*) on the Pacific Coast of North America



Gerald G. Singh^a, Iain McKechnie^{b, c, *}

^a Institute for Resources, Environment and Sustainability, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

^b Department of Anthropology, 308 Condon Hall, University of Oregon, Eugene, OR 97403, USA

^c Department of Archaeology, Hakai Institute, Simon Fraser University, Burnaby, BC V5A 1S6, Canada

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ABSTRACT

California mussel (*Mytilus californianus*) are ubiquitous shellfish species in coastal archaeological sites throughout western North America but are often highly fragmentary when recovered in small-volume 'column' or 'bulk' samples typically used to quantify shellfish assemblages. Archaeological research has predominantly focused on evaluating the dietary contribution of *Mytilus* but most studies assume an average meat weight or use categorical size classifications to determine subsistence strategies and harvest profiles. In this paper, we develop and evaluate a regression-based method for estimating shell length and meat weight for fragmentary *Mytilus* remains. Our regressions are based on live-collected *M. californianus* specimens from multiple locations in California and British Columbia and provide considerable statistical confidence for predicting length and meat weight. We also apply the same regressions to a collection of *Mytilus trossulus* and show similar predictive equations, indicating this method can be used in cases where it is not possible to distinguish morphologically between *M. californianus* and *M. trossulus*. We demonstrate how these results improve upon previous size-classification methods and discuss the potential for applying these measurements to enhance the relevance of these zooarchaeological data for modern marine conservation and management efforts.

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1. Introduction

The California mussel (*M. californianus*) is a ubiquitous and protein rich shellfish species found in archaeological sites throughout the coast of western North America (e.g., Braje et al., 2007; Erlandson, 1988; Losey and Power, 2005; Porcasi, 2011; Sumpter, 2005). Mussels are present from the mid-to lower intertidal on wave-exposed rocky coasts from Alaska to Baja California (Schmidt, 1999; Suchanek, 1979). Judging from the ubiquity and abundance of *M. californianus* in coastal archaeological assemblages as well as numerous ethnographic accounts of its use, this species was a widely valued marine food regularly harvested and consumed by coastal indigenous people throughout the Holocene (Braje et al., 2012; Ellis and Swan, 1981; Erlandson et al., 2008;

Jones and Richman, 1995; Whitaker, 2008). Mussels are considered 'ecosystem engineers' in intertidal ecosystems, providing habitat for many invertebrates and outcompeting intertidal seaweeds (Menge et al., 1994; Paine, 1974). *M. californianus* can be long-lived (>20–50 years) and grow to large sizes (over 20 cm in length) and thus can be overharvested by humans (Seed and Suchanek, 1992). Ecologically, *M. californianus* populations respond to a variety of factors such as climate and oceanography (Menge et al., 2008; Smith et al., 2006), temperature (Ford et al., 2010; Harley, 2011), and intertidal predation by other marine predators such as sea stars (*Pisaster* sp.) and sea otters (*Enhydra lutris*) (Menge et al., 1994; Singh et al., 2013). Given the ecological and economic importance of mussels, further investigation into the characteristics of archaeological assemblages has the potential to enrich understanding of coastal adaptations, human–environment interactions, and paleoecology.

Coastal archaeologists have a long history of investigating archaeological shellfish assemblages to detect nutritional, cultural, and ecological patterns and changes over time (Cook, 1946; Moss,

* Corresponding author. Department of Anthropology, 308 Condon Hall, University of Oregon, Eugene, OR, 97403, USA.

E-mail addresses: geraldsingh@gmail.com (G.G. Singh), iainm@uoregon.edu (I. McKechnie).

1993; Nelson, 1909; Shawcross, 1967; Swadling, 1976; Waselkov, 1987). On the Pacific Coast of North America, the bulk of archaeological research on *M. californianus* has predominantly occurred in California where analysis has focused on the assessment of dietary importance (Erlandson, 1988; Glassow and Wilcoxon, 1988; Greengo, 1951; Treganza and Cook, 1948), harvesting strategies (Jones and Richman, 1995; Whitaker, 2008), and seasonality (Eerkens et al., 2013; Jew et al., 2014; Jones et al., 2008). Archaeologists have additionally utilized archaeological *Mytilus* sp. for informing environmental and sea level changes (Graham et al., 2003) and the impact of long-term sustained human harvests (Botkin, 1980; Braje et al., 2012).

In contrast, shellfish research on the Northwest Coast has rarely focused on *M. californianus* despite its ubiquity in archaeological assemblages (Cannon et al., 2008; Clarke and Clarke, 1980; Croes, 2005; Orchard, 2009; Sumpter, 2005; Wessen, 1988). Rather, the bulk of shellfish research has focused on clams, specifically the seasonality of clam harvesting (e.g., Burchell et al., 2013; Croes, 2005:111; Ham and Irvine, 1975; Keen, 1979; Maxwell, 2003; Wessen, 1982:144).

Mussels can exhibit wide size variation that is nutritionally and ecologically meaningful. However, the occurrence of whole shellfish is rare in most depositional settings (Faulkner, 2011; Muckle, 1985; Wolverson et al., 2010) and this is particularly the case for *Mytilus* (Ford, 1992; Glassow, 2000). *Mytilus* survivorship may be further influenced by excavation and post-excavation sample processing (e.g., wet/dry screening, sorting, and curation). Measurements of complete 'whole' shells are possible given a targeted recovery strategy undertaken during excavation and suitable depositional circumstances such as rockshelter excavations (Croes, 2005:110). An additional potential taphonomic factor in relying on measurements from whole shells is that larger shells may be more robust and thus preserve more readily. Conversely, it is also possible that smaller shells, with less surface area and/or differing shapes, may be less likely to fracture from compaction and trampling (Muckle, 1985; Wolverson et al., 2010).

While a number of studies have developed regression-based methods for evaluating the size distributions of marine and freshwater mussels (Buchanan, 1985; Campbell, 2014; Hall, 1980; Parmalee and Klippel, 1974; Randklev et al., 2009), to our knowledge, the Pacific coast of North America currently lacks a regression-based method for determining *M. californianus* shell length and no method has estimated meat-weight from fragmentary remains (Bell, 2009:25; but see Ford, 1989:161 for an example specific to *Mytilus trossulus*). As a result, the majority of research concerning archaeological *M. californianus* has relied on 'average' meat weight contributions from 'average sized' mussels (Cook, 1946; Croes and Hackenberger, 1988:36; Kennedy, 2004; Mitchell, 1988; Moss, 1989). In a few cases, length measurements obtained from whole shells have been reported (Braje et al., 2012; Croes, 2005:110; Erlandson et al., 2008) but these remain rare relative to the more commonly quantified assemblages focused on bulk or column samples (e.g., Glassow, 2000; Moss, 1993; Sumpter, 2005).

1.1. Categorical size classification methods

The lack of a regression based measurement is significant as the majority of shellfish examined from intensively quantified small-volume bulk samples are fragmentary which constrains the ability to generate robust harvest profiles from these painstakingly calculated proportional data. This circumstance also limits the accuracy of derived secondary information, such as estimates of 'meat weight' calculated from non-repetitive element counts (NRE) (Giovas, 2009; Mason et al., 1998) or the effect that shell size may

have on the proportional frequency of weighed shell fragments (Glassow, 2000).

Some researchers have provided estimates of *Mytilus* shell length using size categories to construct cumulative harvest profiles to identify size selectivity (Wessen, 1982:151). For instance, research on *M. californianus* by Whitaker (2008) has built on a size classification method developed by White (1989) and Jones and Rickman (1995) to document the harvest profile for fragmentary mussels from a rockshelter assemblage in Northern California. White's (1989) method involves comparing archaeological mussels to traced outlines of 2-cm length categories in which researchers place fragmented mussel umbos onto a two-dimensional template with traced outlines of a particular size. Researchers visually match the valve shape and size that best fits the template. The resulting size assessment is used to categorize archaeological valves and then analyzed in a cumulative harvest profile where it can distinguish differences in prey selectivity (e.g., size selective 'plucking' or indiscriminant stripping and variations in between).

Bell (2009) subsequently evaluated this classification method and demonstrated considerable statistical uncertainty in this approach, particularly when applied to fragmentary valves, which weakened predictive accuracy. A key recommendation was to develop a more accurate estimation of total shell length based on morphometric relationships from fragmentary remains as has been demonstrated for mussels elsewhere (Campbell, 2014; Hall, 1980; Randklev et al., 2009).

In this study, we develop and evaluate a morphometric regression method for deriving total length estimates from incomplete *M. californianus* shells. Our method offers a variety of measurements that predict the length of fragmentary shells with considerable statistical confidence. Regressions are based on live mussels collected from multiple areas of California and British Columbia and thus relevant for archaeological application across this broad coastal region. Given these regions are subject to varying climatic and oceanographic conditions, incorporating this variability helps the resulting regressions better account for differential growing conditions and climatic changes. We conclude this improves the basis for investigating harvest profiles, measures of *Mytilus* biomass represented archaeologically, and the historical ecology of this widespread and important shellfish genus.

2. Materials and methods

2.1. Sample selection

To derive and evaluate biometric relationships, 132 live *M. californianus* were collected from numerous intertidal plots within three exposed coastal embayments on western Vancouver Island, British Columbia, Canada as well as ecological collections from Northern and Southern California, USA (Fig. 1, Supplemental materials). Mussels were obtained from the mid-to-low tide on wave-exposed rocky shores as part of a marine ecology research project seeking to control for growth variation along this latitudinal gradient (Helmuth et al., 2006; Singh, 2010; Singh et al., 2013). This broad spatial scale is relevant as it accounts for multiple environmental and growing conditions across space and therefore serves as a proxy for variability in growing conditions across broad temporal scales (e.g., Pickett, 1989). Climatic variables, especially temperature and tidal elevation, has a strong effect on mussel growth rate (Harley, 2011; Menge et al., 2008; Seed and Suchanek, 1992; Suchanek, 1981) and different growth conditions can lead to differences in size as well as variation in shell morphology. Thus, our regressions aim to incorporate uncertainty across this large region as such uncertainty is likely to occur over archaeological time scales.

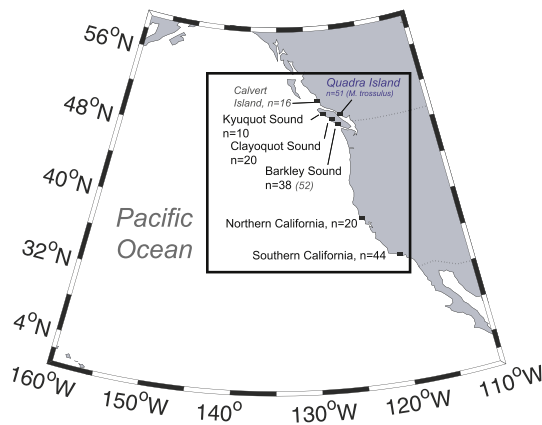


Fig. 1. Map showing locations and sample numbers of *M. californianus* and *M. trossulus* specimens collected for this study. Italicized sample numbers represent beach collected shells used to evaluate taphonomic effects as discussed in the text.

2.2. Measurement criteria

For each individual mussel used to derive the regression equations, we measured a series of points from the umbo to morphologically distinctive markers on the shell (e.g., the hinge teeth on the inside of the shell) (Fig. 2). We measured these attributes because they form the most robust portion of the shell and are more readily recovered in small volume archaeological samples that are typically the focus of detailed quantification efforts.

The umbo region of mussels is also the oldest site of growth (Ford et al., 2010; Seed, 1968). From this point, individuals add layers via secretions from the mantle to the inner side of the shell (from the umbo to the distal end of the shell) (Checa, 2000). The robusticity and thickness of the umbo increases as the mussel ages while the ligament (hinge) connecting the two valves of the shell also increases in length as the mussel increases in size. Despite the potential for allometric variation in growth within a particular

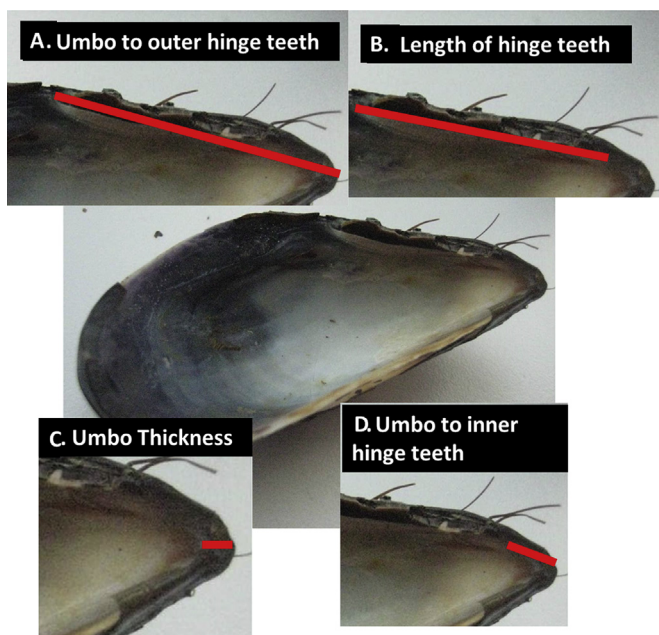


Fig. 2. Measurements made on a shell of *M. californianus* (main and inset pictures) to create regressions to predict total shell length. Measures of the lengths of A–D were made with the total length of the shell. The photo shows the inside of the left valve.

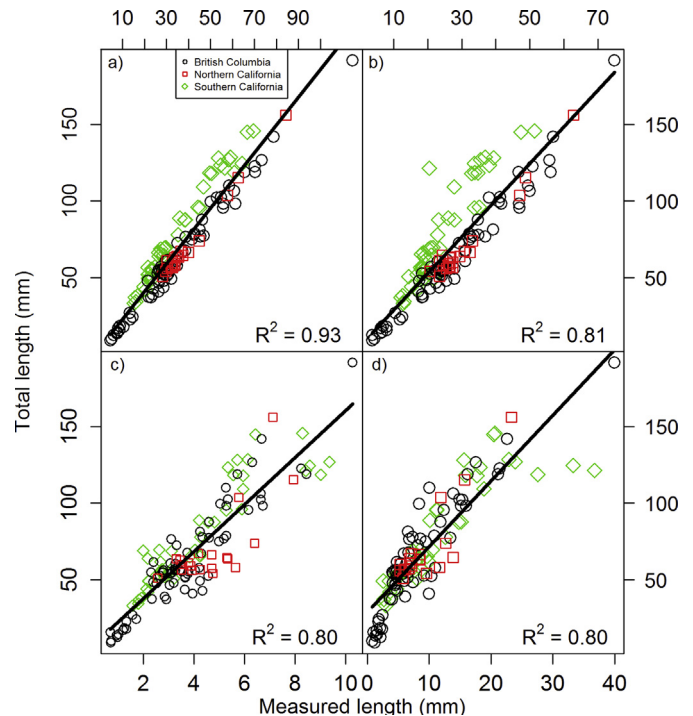


Fig. 3. Regression model fits to data. Different colored and shaped points correspond to shells collected in different areas (refer to legend). a) Umbo to far hinge teeth. b) Length of hinge teeth. c) Umbo width. d) Umbo to near hinge teeth. Letters correspond to measurements shown in Fig. 2.

habitat, these characteristics make the measurements appropriate for morphometric regression with a reasonable degree of accuracy.

To maximize measurements obtained from a given archaeological assemblage (e.g., fine and coarse mesh fractions), we measured multiple dimensions on individual mussel shells to account for shells in different states of fragmentation (Fig. 2). Although this method yields regressions with differing predictive strengths, these uncertainties can be quantified. A particular benefit is that the umbo is used to derive minimum number of individuals (MNI) or non-repetitive elements (NRE), which are especially prevalent in small mesh sizes (Glassow, 2000:410). Thus deriving length estimates from these fragmentary specimens can considerably strengthen the analytical potential of these rigorously quantified assemblages and the ecological relevance of data derived from them.

We use simple ordinary least squares regression to build the predictive models (Table 1). For fragment samples that are large enough to take multiple measures, we also provide multiple regression model structures for incorporating multiple measures

Table 1

Regression equations for estimating total length of mussel shells from shell fragments. The accuracy measurements are a measure of how different, on average across sizes and participants, the estimate is from the actual total shell length, and represents the mean error as well as the 95% confidence interval.

Measurement description (x)	Regression equation	R ² value	Average error (±95% CI) in double blind trials
Umbo to outer hinge teeth	Total length = 1.8074 x + 4.947	0.93	7.3 ± 1.2 mm
Length of hinge teeth	Total length = 2.3916 x + 4.9349	0.81	11.2 ± 1.9 mm
Umbo thickness	Total length = 15.312 x + 7.1701	0.80	10.2 ± 1.9 mm
Umbo to inner hinge teeth	Total length = 4.284 x + 28.94	0.80	12.8 ± 3.0 mm

into making an estimate. These multiple regression models explain variation slightly better than the simple models (as indicated by the R^2 values in Table 2) and can offer an extra level of confidence in the estimation for particular shells if warranted.

2.3. Meat weight estimates

Our linear regression models are related to total shell length and the predictive confidence is a corresponding R^2 value. Since our regressions are based on live-collected mussels, we additionally calculated dry meat weight for each specimen (distinguishing gonads and non-reproductive tissue). Thus, we also were able to derive a strong shell length-meat weight relationship, which can be applied to a derive minimum weight estimates from individual archaeological *M. californianus* specimens.

2.4. Evaluation of taphonomic effects

In addition to the live-collected specimens that form the basis of the regression, we conducted these same measurements on 68 *M. californianus* valves recovered from the upper intertidal ‘wrack zone’ in two locations in British Columbia (Barkley Sound and Calvert Island, Fig. 1, Supplemental materials). These beach-collected shells represent natural mortality events induced by wave action during storms, following years (or at least several months) of weathering and erosion as shells are transported to upper intertidal beach deposits. These weathering and wave induced erosional processes can be considered broadly similar to the taphonomic processes affecting archaeological shells over broader time scales (e.g., trampling, erosion of prominent surfaces etc.) (Muckle, 1985). While not directly analogous to other post depositional effects such as leaching (Stein, 1996), we used the simple regression models to estimate total size of these beach collected shells. This was done in order to assess model performance on weathered shells as well as to evaluate the accuracy of measurements obtained on archaeological shells that may have been subject to weathering and wave erosion following depositional in nearshore contexts (i.e., deposition or re-deposition from a formerly upper intertidal context).

2.5. *Mytilus trossulus* measurements

Despite a considerable maximum size difference, *M. californianus* is morphologically similar to the ‘Bay’ mussel (*M. trossulus*, formerly referred to as *Mytilus edulis*) and it is often difficult to distinguish the two taxa based on small fragments. Thus, many archaeological analyses cautiously lump all *Mytilus* specimens into a single category (even umbo fragments) unless local environmental conditions preclude the presence of either. To assess the potential biometric difference and or complementarity between *M. californianus* and *M. trossulus* growth, we conducted measurements on 51 *M. trossulus* shells collected from protected beaches on Quadra Island in the

northern Salish Sea (Fig. 1, Supplementary data). This inland sea is situated far from the exposed Pacific Coast in habitat unsuitable for *M. californianus*. Unlike the wave-transported beach collected shells described above, *M. trossulus* valves were collected at low–low tide from a very protected beach with a lack of wave exposure (Heriot Bay, BC). These shells exhibited a lack of weathering and erosion and appeared to be recently deceased as they were obtained directly below piers or elevated rocky crevices on which live clusters of *M. trossulus* were growing. The simple regression models developed for *M. californianus* were applied to these *M. trossulus* shells to determine how well they perform on these morphologically similar species.

2.6. Model validation

To assess the accuracy and potential inter-observer bias for our measurements and the resulting regressions (e.g., Lyman and VanPool, 2009), we conducted double-blind trials that compared differences in the estimates of total mussel length between multiple participants (Table 1). Using a separate population of mussel shells from those used to develop our relationships or our beach collected samples ($n = 54$), we recorded total lengths of individual shells identified with numeric codes and subjected them to destructive fragmentation. Individual umbo fragments obtained from this ‘crushed assemblage’ were then given to multiple participants to evaluate both our regression method as well as the size classification method developed by White (1989). Accuracy of size predictions was evaluated by comparing predicted lengths with known lengths, with average differences between these measures and average inter-observer differences reported and graphed along a 1:1 line (Table 1, Fig. 4).

3. Results

All regressions based in reference to the umbo showed a strong predictive relationship, indicating a very strong fit of the model to the data and thus a strong relationship between the linear measures and the total shell length (Table 1). The R^2 values of the regressions range from 0.80 to 0.93, meaning that between 80 and 93% of the variability in mussel lengths is accounted for by the linear regression model, indicating that these models are good predictors. These linear relationships are consistently strong despite regional variability in morphology or growing conditions. We note slight differences in rates of growth, with Southern California being the most distinctly offset (i.e., diamonds in Fig. 3). However, given that we are interested in incorporating variation in growing conditions as well as paleoclimatic variation, we included data from all regions to generate these predictive models.

We also noted that the relationship between total shell length and the dry weights of gonads, non-reproductive body, and shell offer strong relationships, albeit nonlinear (Fig. 5). Linear models are more likely to systematically underestimate weight for both small and large shells as well as potentially yield negative weight values for the smallest shells (i.e., there is no negative intercept in our non-linear model). We found that our models explained between 78 and 90% of the variation in body mass, depending on tissue type (reproductive and non-reproductive), while relating total length to total dry meat, the predictive model for weight accounts for 90% of the variation (Table 3, Fig. 5).

3.1. Testing categorical models

Bell (2009) noted that White's (1989) method of size categorization has limited predictive power, particularly between estimated length and total shell length. Similarly, our comparison of

Table 2

Multiple regression models incorporating multiple measurements. In cases where enough of the shell is intact enough to make multiple measurements (the two cases are described under the ‘Shell Fragment’ column), these models can be used to obtain increased accuracy in length estimates than with simple regressions shown in Table 1.

Shell fragment	Regression equation	R^2
Can see hinge teeth closest to umbo	Total length = 8.2384 (umbo) + 2.2361 (inner hinge) + 14.8106	0.84
Can see entire length of hinge teeth	Total length = -0.9582 (umbo) + 2.0493 (inner hinge) + 0.8868 (hinge length) + 0.6065 (far hinge) + 8.4309	0.94

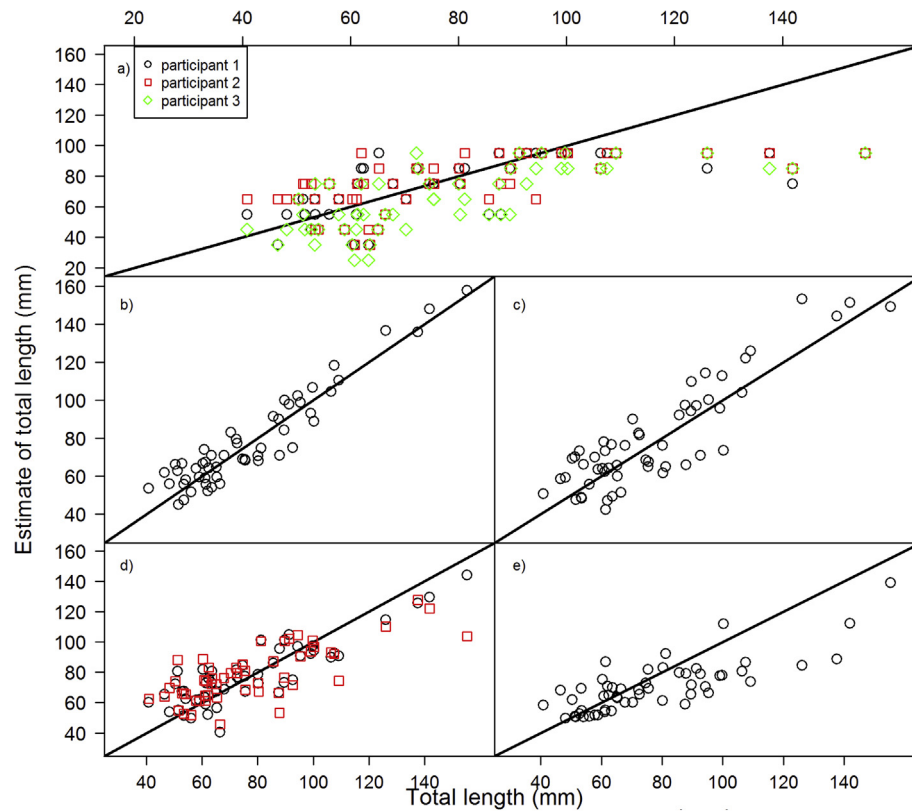


Fig. 4. Visual comparison of estimated total length to known shell lengths using a) White's (1989:133) template, b) the regression model based on measuring the length from the umbo to the outer hinge teeth, c) the regression model based on measuring the length of the hinge teeth, d) the regression model based on measuring the width of the umbo, and e) the regression model based on measuring the length from the umbo to the inner hinge teeth. The straight lines are not regressions in themselves, but instead represent a 1:1 relationship, with the best models falling along the line. Model predictions that are more accurate fall closer to the straight line, while those points farther away represent relatively worse predictions.

the difference between estimated shell lengths and actual shell lengths produced by White's (1989) template indicates an average error of 16 ± 3 mm (Fig. 4). White's template was unable to estimate mussel shells above 100 mm because the template categories did

not go above this range. This is indicated in Fig. 4a by the wide distributions of actual shell lengths estimated in the 90–100 mm range, though many are larger than 100 mm. Comparatively, the average error between the predicted and actual shell lengths range from 7.3 to 12.8 mm across shell sizes in the double blind trials using our regression models (Table 1, Fig. 4b–e). The model based on the measure from the umbo to the outer hinge teeth was the most precise (Fig. 4b), having an average error of 7.3 mm. Our double-blind results demonstrate that there is considerable inter-observer variability between researchers measuring the same specimens using White's method, which further confounds its predictive power (Fig. 4a). Our results indicate the accuracy of White's method, on average across all participants, was 9.5 ± 1.5 mm between analysts. By contrast, the precision of our estimates, using the umbo thickness model (a modestly performing

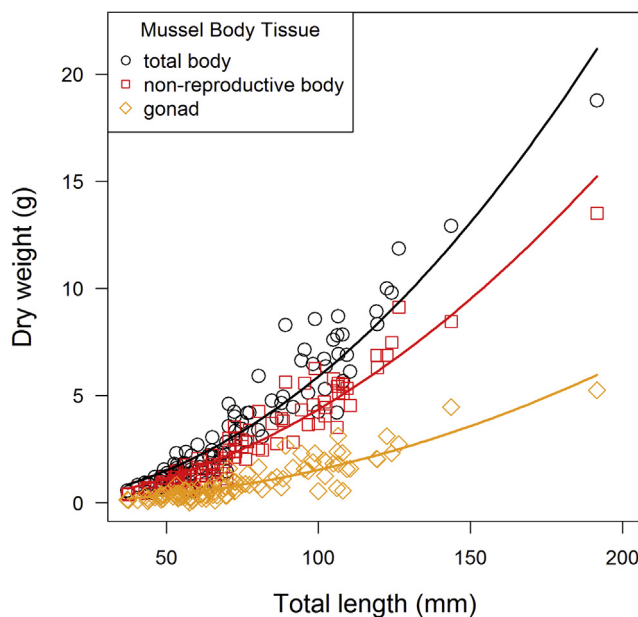


Fig. 5. Relationships between total length and dry weight mass for reproductive, non-reproductive, and total meat weight.

Table 3

Regression equations to estimate dry body (meat) weight from total shell length for *M. californianus*.

Estimate	Regression equation	R ²
Dry weight of total body	Dry weight = $0.0006832 \times \text{total length}^{1.9678096}$	0.89
Dry weight of non-reproductive body	Dry weight = $0.0006155 \times \text{total length}^{1.9249686}$	0.90
Dry weight of gonad	Dry weight = $0.0001019 \times \text{total length}^{2.0887239}$	0.78

regression), averaged between all participants, indicates that measurements were off by 5.1 ± 2.3 mm between analysts.

3.2. Beach collected shells

The simple regression models predicted total length of weathered, beach collected shells with similar accuracy compared to the fresh shells, with mean error between 5.4 and 15.4 mm from the actual lengths of shells (Table 4). Models based on the length from the umbo to outer hinge teeth, length of hinge teeth, and umbo thickness were slightly more accurate for beach collected shells, and the model for umbo to inner hinge teeth was slightly more accurate for fresh shells, but in every case the error estimates had 95% confidence intervals that overlapped, indicating no significant difference in performance between fresh shells and beach collected shells.

3.3. *M. californianus* and *M. trossulus*

Evaluating the performance of the four simple regressions developed for *M. californianus* as applied to *M. trossulus* indicates that these models predict total length of shells as accurately as, and in some instances, more accurately for *M. trossulus* (Table 4). The models based on 'umbo to outer hinge teeth' and 'hinge teeth length' performed better for *M. trossulus*, and the non-overlapping 95% confidence intervals indicate that they perform significantly better than for live collected *M. californianus* shells, though the 95% confidence intervals overlap with the beach collected shells.

4. Discussion

Our morphometric regressions provide a more accurate method for confidently estimating the total shell length from mussel umbo fragments relative to the size-class method utilized by Wessen (1982), White (1989), and applied by Whitaker (2008) and others. This is further apparent in a reduction in the variability in length estimates between analysts and an expansion of length estimates of *M. californianus* on continuous interval scale across their size spectrum (including mussels >200 mm) in contrast to White's template which appears limited to *Mytilus* less than 100 mm (White, 1989:133). Additionally, incorporating shells from multiple geographic regions subjected to multiple growing conditions is arguably more relevant for application to archeological assemblages across a spectrum of climatic conditions and ecological settings.

These models offer more reliable estimates for meat-weight for *M. californianus* than previous research utilizing average weights and calorie estimates (Croes and Hackenberger, 1988:36; Erlandson, 1988:104). Due to the high rate of fragmentation for *Mytilus* (Glassow, 2000; Muckle, 1994), these methods likely also provide a much more representative range of size distributions than measurements of comparatively rare whole *Mytilus* valves suitable for measurement (Erlandson et al., 2008). Measured shell umbo fragments can provide estimates of the total length, as well as the dry weight (differentiated between tissue types). Combined

with archaeological measures such as minimum number of individuals (MNI) or non-repeatable elements (NRE) (Giovas, 2009), these models provide the opportunity to refine estimates of meat-weight and *Mytilus* biomass from archaeological samples. Given the good performance of the length models on *M. trossulus* as well, it is possible to derive meat weight estimates from fragmentary remains using available shell length to meat weight regressions for *M. trossulus* (e.g., Penney et al., 2008), and thus generate species-specific bounded estimates of meat weight per sample.

Surprisingly, our models are similarly accurate in estimating total length for moderately beach-weathered mussel shells, and so still retain strong predictive capacity. This could reflect the robustness of this portion of the shell, and indicate that the morphometric relationships are less affected by taphonomic weathering (i.e. erosion does not strip away shell thickness on the scale of multiple millimeters). These observations provide a measure of confidence that the measurement of archaeological *Mytilus* assemblages that may have been subject to modest post-depositional wave erosion retain their predictive accuracy. The models also showed strong potential for estimating total length of *M. trossulus* shells. In some cases the models performed better for smaller mussels, and this could be due to the fact that *M. trossulus* has a notably narrower growth range and/or their size distribution falls in a zone where more samples fit the model (and therefore the areas of the model that are more certain). This result highlights how both *Mytilus* species have very similar morphology and morphometric growth relations, and therefore estimates can be combined in cases of taxonomic uncertainty. Overall, the favorable performance of the models across a wide range of specimens (multiple species, various stages of erosion, and locations of collection) highlight the broad applicability of the models and the general approach we advocate.

This method is not devoid of uncertainty but represents a significant improvement from size-class data. Based on our trials, our models estimated the maximum error in total lengths as high as 35 mm different from the actual length in individual cases but this is compared to an error of 67 mm using White's (1989) template. Even so, on average, our results indicate that our models produce more certain results based on average error (7.3–12.8 mm with our models versus 15.8 mm with the template). More importantly, a regression based approach provides the ability to transform shell length estimates from categorical data (binned size classes) into continuous data therefore increasing the analytical utility through improved quantification of uncertainty and comparison across multiple datasets (e.g., layers within sites, between individual sites, regional trends).

By sampling over a broad geographic area of the eastern Pacific coast, we have sought to incorporate climatic variation in our models. However, mussels from archeological samples remain likely to have grown in conditions outside what we have sampled for this study (Harley, 2011). Future research may reduce the uncertainty in our models and/or create regionally specific models should research questions require it. We encourage researchers to contribute to improving this morphometric approach by making their primary measurement data available as we've done here (see Supplementary data).

Which relationship to use will largely depend on how much of the shell remains intact. The model using the measurement from the umbo to the outer hinge teeth had the strongest fit ($R^2 = 0.93$) but requires most of the shell to be intact. The model that accommodates the most fragmentary shells (umbo thickness), still yields an estimate of shell length with moderately strong predictive power ($R^2 = 0.80$, Table 1). This is the measure that will likely be most useful for archaeological applications given this is the thickest part of the shell and mostly likely to preserve. While this may only

Table 4
Mean error estimates of the four different regression models used on beach collected *Mytilus californianus* shells and shells of *Mytilus trossulus*.

Shell type	Umbo to outer hinge teeth	Hinge length	Umbo thickness	Umbo to inner hinge teeth
Beach collected	5.4 ± 1.4	9.5 ± 2.3	9.9 ± 2.3	15.4 ± 3.4
<i>M. californianus</i>				
<i>Mytilus trossulus</i>	4.0 ± 1.2	5.9 ± 1.3	9.5 ± 3.1	15.5 ± 3.6

represent a modest improvement in accuracy from existing size classification methods, it is capable of generating length estimates for a larger range of shell sizes and is applicable to a greater range of fragmentary umbos. This method therefore enables a larger number of measurements to be obtained for a given deposit with a greater predictive accuracy. Moreover, if it is possible to obtain more than one measurement on a given shell, multiple regression models can be used to further strengthen length and or meat-weight predictions (Table 2). This latter approach might be of particular interpretive value for an individual shell (e.g., an artifact) or for more confidently establishing an upper size threshold.

More important than the statistical power of individual measurements is the interpretive confidence needed for a given research question. In this respect, existing size classification methods may perform adequately for interpretations such as Whitaker's (2008) comparison of *Mytilus* harvest profiles in relation to idealized foraging theory models. However, such measurement data may not be appropriate for statistical analysis that surpasses an ordinal scale (Wolverton et al., 2014). The broader utility of our morphometric approach is an increase in predictive accuracy, reduction in inter-observer error, and a comparatively more straightforward data output (individual size estimates and an associated uncertainty).

Collectively, the method can be used to more precisely measure *Mytilus* size distributions and test for statistically significant differences at different points in time or between sites. Of particular ecological relevance is evaluating the size distribution in relation to the long-term presence of sea otters which have been shown to homogenize mussel sizes through regular harvesting and elimination of larger and older *M. californianus* (Singh et al., 2013). Sea otters (*Enhydra lutris*) are voracious consumers of mussels (VanBlaricom, 1988), and the methods we provide can potentially be used to evaluate if mussel size distributions were altered when sea otter remains are found in temporally associated midden strata (e.g., Simenstad et al., 1978; Szpak et al., 2012).

Analysis of shell lengths can also be used to revisit the question of the *Mytilus* harvesting and cultivation practices of Indigenous peoples as investigated by Whitaker (2008). This method provides a means of refining the statistical characterization of a 'plucking' strategy (the preferential size selection of larger mussels) versus a 'stripping' strategy (indiscriminant removal of a variety of size classes) (Jones and Richman, 1995; Whitaker, 2008). Alternatively, measuring size distributions may also help characterize periods of change in ocean upwelling as reflected in size distributions before, during, and after known climate changes (e.g., Kennett and Kennett, 2000), the short term impacts of intensive human harvesting (Croes, 1992; Thakar, 2011), or the potential restraint exercised in traditional clam management practices (Cannon and Burchell, 2009; Daniels, 2014; Lepofsky et al., 2015). While our method provides improved measurement capacity, disentangling such factors will require multiple lines of evidence and a consideration of the causal agents that can produce similar size distributions.

While a variety of size-based regressions have been applied to a variety of archaeological shellfish taxa elsewhere (e.g., Jerardino and Navarro, 2008; Parmalee and Klippel, 1974), additional models for other species are needed on the Pacific Coast in order to refine estimates of dietary content and biomass represented in shellfish assemblages. For instance, clams are another pervasively utilized shellfish that are commonly abundant in shell midden settlements (Cannon et al., 2008) and similar methods have begun to be variously developed for clams at specific sites (Daniels, 2014; Ford, 1989:161), but this can usefully be expanded to include more species and more geographically representative locations.

5. Conclusion

This paper has developed and evaluated a method for *Mytilus* shell length estimation for application to archaeological and ecological research in western North America. This method seeks to improve the precision of zooarchaeological data in order to enhance the interpretive potential and historical ecological significance of archaeological shellfish assemblages (Rick and Lockwood, 2013). Future application of this low cost and relatively straightforward method has the potential to increase the number of archaeological assemblages available for metrical comparison and assessment, well beyond the small number of sites where *Mytilus* length distributions have currently been obtained. Given the importance of shellfish in the archaeological record along the eastern Pacific Coast and the long history of archaeological analysis, improving the capacity to obtain metrical data from existing quantified assemblages will provide for a more thorough integration of ecological and archaeological data. While the method improves coastal archaeologists' ability to address existing archaeological questions such as dietary contribution and harvest and management strategies, it also brings zooarchaeological information more directly into conversation with a variety of research in ecology, conservation biology, and resource management (e.g., Erlandson and Rick, 2010; Wolverton and Lyman, 2012). Thus, rather than just another technically challenging and expensive analytical method requiring reallocation of scarce funding resources, this study aims to increase the utility of data derived from conventional shellfish quantification methods and strengthen the analytical effort of thousands of person hours spent counting and/or weighing shell fragments.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jas.2015.02.029>.

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