Shell morphometry of seven limpet species from coastal shell middens in southern Africa

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Abstract

Measurements of shell parts and features (elements) of marine limpets can be used to derive morphometric equations for estimating total shell lengths. This is demonstrated for seven limpet species commonly found on the southern African coast. The equations can be used to reconstruct whole shell lengths for highly fragmented limpet samples in prehistoric shell middens. A linear regression model is based on measurements of all shell elements, resulting in high coefficients of determination with excellent predictive power in most cases. These morphometric equations would enable archaeologists to derive more metrical information from fragmentary archaeological material than was previously the case. We also present a case study where morphometric equations of two limpet species are applied to an archaeological sample from the South African west coast for the purpose of investigating possible biases in limpet shell preservation. We conclude that small whole limpet shells survive longer than the bigger ones in this particular case, but that many more such case studies need to be conducted in order to fully understand differential preservation of southern African limpet shells in archaeological sites.

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1. Introduction

Archaeological sites on the south and west coasts of South Africa have received increasing international attention in recent years thanks to discoveries of Middle Stone Age (MSA) components with early remains of anatomically modern humans, as well as elements of material culture that point to early modern human behavior (Erlandson, 2001; Grine et al., 1998; Henshilwood et al., 2001, 2002; Rightmire and Deacon, 2001; Singer and Wymer, 1982). The uppermost levels of these deep, stratified deposits sometimes overlap the bases of several equally deep Later Stone Age coastal sites, and together they now form the very backbone of southern Africa’s Stone Age sequence (Deacon and Deacon, 1999; Deacon and Geleinjse, 1988; Fagan, 1960; Goodwin, 1938; Goodwin and Malan, 1935; Inskeep, 1987; Klein, 1972; Marean et al., 2000; Shire, 1962; Singer and Wymer, 1982; Thackray, 2000; Volman, 1981; Wurz, 2002). They also provide data from which long-term palaeoenvironmental changes have been inferred (Avery, 1987; Cowling et al., 1999; Klein, 1972; Klein and Cruz-Uribe, 1987, 1997, 2000; Parkington et al., 2000; Shackleton, 1982; van Andel, 1989).

Overall, these sites provide insights into the cultural sequence and environmental background of Upper Pleistocene and Holocene indigenous societies, particularly the changing patterns in procurement of marine resources as sea-level recovered from its lowest mark during the Last Glacial Maximum (Inskeep, 1987; Klein, 1972; Parkington, 1981). Along the South African West Coast, such changes nicely track records of sea-surface temperature and sea-level changes for the southern Atlantic (Cohen et al., 1992; Jerardino, 1993).
There are parallel increases in the forager population and residential permanence, increased consumption of marine resources, and local depletion of at least three species of gastropods within the last 3500 years (Jerardino, 1996; Jerardino et al., in press). Additional dietary and anatomical patterns have been derived from Holocene human skeletons recovered from the west and south coasts (Lee-Thorp et al., 1989; Pfeiffer and Sealy, 2006; Sealy and Pfeiffer, 2000). Other coastal sites have also provided key evidence that mark the introduction of pastoralism to southernmost Africa (Henshilwood, 1996; Sealy and Yates, 1994; Vogel et al., 1997). Thus, coastal sites have played a major role in the reconstruction of pre-colonial history of southernmost Africa, and continue to do so.

Quantitative and metrical analyses of marine invertebrate remains have provided both central and contextual evidence for the above reconstructions, a task which has often not been easy due to the fragmentary nature of archaeofaunal material. Fortunately, morphometric equations have been established for two species of mussels (Buchanan, 1985; Hall, 1980) and one species of crustacean (Jerardino et al., 2001), which have resulted in productive applications to archaeological case studies (Jerardino et al., in press; Thackeray, 1988).

Typical of the problem are the limpets *Cymbula* and *Scutellastra*, which are known to survive in South African shell middens, but often in statistically inadequate numbers. Archaeologists are thus forced to hugely increase overall sample size and also collect intact shells from material not sampled for marine shells in order to recover enough unbroken shells of these fragile taxa for measurement (Jerardino, in press). But excavations are increasingly faced with time and financial constraints that inhibit the recovery of voluminous shell samples. Planning and budgeting for a sampling strategy that maximizes the recovery of whole limpet shells is made doubly difficult by our inability to predict the degree of shell fragmentation ahead of excavations, let alone shell density, or the extent to which the shells will be cemented in hard matrix as often occurs in MSA components (Klein et al., 2004; Meean et al., 2004; Volman, 1978). Added to these concerns is the uncertainty whether the limpet size record based on whole shells is biased in any way. An argument could be made that larger limpets will survive better in shell midden deposits than smaller ones, thus inflating the mean length of the whole limpets recovered. A counter-argument would hold that small limpets can hide and be protected under larger shells and other spaces, and are thus less likely to fragment in situ. Consequentially, mean length of whole limpets will distort in favor of smaller overall size. Because morphometric equations yield measurements from fragments, the potential biases introduced by measuring only whole limpets are eliminated.

The best way to overcome these problems is to develop morphometric equations for shells that allow the estimation of shell lengths from easily recognizable shell parts or shell features that survive in the highly fragmented archaeological record. Here, we propose suitable parameters of morphometric equations for seven limpet species commonly found at coastal sites in southern Africa, and apply some of these in a case study involving two of the most dominant limpet species (*C. granatina* and *S. granularis*) found in shell middens along the West Coast of South Africa. This case study is aimed at not only showing how sample sizes of shell measurements are increased with the use of fragmentary material. Here we take it further to check for possible preservational biases.

### 2. Materials and methods

The control samples used in this study were recently collected limpets in the reference collections of the Departments of Zoology and Archaeology at the University of Cape Town, and of IZIKO: South African Museum, Cape Town. Collection records show that most of the control specimens were collected live. A few with badly eroded apices, probably caused by wave action, were rejected. Table 1 shows the numbers of shells analyzed for seven different species, and the size ranges of each sample. None of the samples represents single localities. Instead, the geographic spread of collected specimens within each sample reflects the overall modern distribution of the species (Branch et al., 1999; Kilburn and Rippey, 1982). The one exception is the *S. granularis* sample, in which most shells came from just two locations on the West Coast, although its natural range extends much farther along south and east coasts where relatively warmer sea surface temperatures prevail (Kilburn and Rippey, 1982). The west/cold to east/warm temperature gradient appears to covery with the mineralogy and crystalline structure of the shell of *S. granularis*, specifically the thicknesses of calcitic and aragonitic layers within the shell (Cohen and Branch, 1992). However, there is no a priori reason why this trend should affect external shell morphology.

The parts of the limpet shell selected for measurement are shown in Fig. 1. The choice of parts was guided by prior knowledge of typical limpet breakage patterns, also which parts were most likely to survive intact. Layout of the measurements was dictated by general shell shape. More measures could be taken on the star-shaped limpets characterized by prominent, long and, protruding ridges (*C. granatina, S. oculus* and *S. longicosta*). Fewer measures were possible on those with roughly oval bases and characterized by many thin and/or regularly spaced ridges (*S. granularis, S. argenvillei, S. barbara, S. tabularis*) (Fig. 1). Thanks to the prominent lateral ridges of the star shaped limpets, two additional measurements

<table>
<thead>
<tr>
<th>Species</th>
<th>No. of shells</th>
<th>Size range (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. granatina</em></td>
<td>94</td>
<td>20.8 – 96.4</td>
</tr>
<tr>
<td><em>C. oculus</em></td>
<td>112</td>
<td>22.9 – 120.3</td>
</tr>
<tr>
<td><em>S. argenvillei</em></td>
<td>97</td>
<td>28.3 – 95.3</td>
</tr>
<tr>
<td><em>S. barbara</em></td>
<td>82</td>
<td>26.3 – 99.1</td>
</tr>
<tr>
<td><em>S. granularis</em></td>
<td>102</td>
<td>17.3 – 68.9</td>
</tr>
<tr>
<td><em>S. longicosta</em></td>
<td>89</td>
<td>29.5 – 84.5</td>
</tr>
<tr>
<td><em>S. tabularis</em></td>
<td>63</td>
<td>28.0 – 135.1</td>
</tr>
</tbody>
</table>
can be obtained, namely lateral width and lateral inner width. These measurements are more difficult to establish for C. granatina shells larger than 60 mm, as lateral ridges are less pronounced when this species reaches full size.

All measurements were obtained with a 0.05 cm precision caliper. Measurements obtained from the ventral side of shells on all species depend on the proper identification of the inner edge of the myostracum (Ridgway et al., 1998), since many of the measurements on this side use this as a starting and/or end point. The inner edge is sharp and unambiguous in fresh specimens of C. granatina and S. granularis thanks to the brown to red-brown color of shell crystals present in the inner-most area of the shell surrounded by the myostracum. Color contrast in this inner area is not as visually striking in the other five species, although the myostracum (white to pale yellow) nonetheless contrasts with that of the crystals that make up the area contained by it (light blotchy grey to uneven light yellow/beige and white crystals). Moreover, because the myostracum and the area contained by it in fresh samples have different light refraction properties visible to the naked eye, the inner edge appears sharp throughout with no areas of blending or fuzziness.

Recorded measurements were entered into spreadsheets and from these data Model I regressions were conducted with R statistical software, version 2.2.1 (R Development Core Team, 2005). As noted with previous studies (Jerardino et al., 2001), Model I regressions (Sokal and Rohlf, 1969) work on the assumption that the independent variable, namely shell length, is measured without error. As human and instrumental error are unavoidably present in all such measurements, Model II regressions should be preferred for this and similar cases. However, when the interest is on using these models for predictive rather than descriptive aims, Model I regressions should be employed regardless of the violation of this basic assumption (Legendre and Legendre, 1998).

3. Results

Table 2 presents the parameters (a and b) and coefficient of determination ($r^2$) of morphometric equations for the estimation of shell lengths from measurements of the various shell parts for the seven control samples. A linear regression model ($y = a + bx$) fitted the data best for each of the limpet species. The coefficients of determination for all morphometric equations are very high ($\geq 0.75$), which shows their good predictive power. The only two exceptions occur with S. longicosta. The high $r^2$ values for inner length, and inner width for all species are most worthy of note, as these shell parts preserve more often than any of the others in archaeological contexts (A.J., personal observation).

3.1. A case study

C. granatina and S. granularis shells from a large shell sample weighing nearly 11 kg and excavated from square KK2 of ‘Grootrif G’ shell midden (Jerardino, in press) were chosen for this study. After shells were inspected closely, measurements other than inner length and inner width were also obtained given their relatively high survival and the excellent predictive power of their respective morphometric equations. Also, contrary to the case of fresh specimens, the area contained within the myostracum in these particular archaeological S. granularis shells is not always as contrasting, opening the possibility for introducing added error in the measurement of inner length and inner width from these shells. Consequently, measurements of total width and posterior length...
were established for *C. granatina*, and anterior length measurements were also obtained from *S. granularis* shells. In order to test for possible bias in the preservation of limpet shells, the mean sizes based on whole shells were compared against those reconstructed entirely from fragmented shells. The basic tenet in statistical sciences that comparisons are based on independent samples prevents us from comparing mean sizes of whole shells against those based on whole plus broken shells (Sokal and Rohlf, 1969). The statistical significance of any changes in the mean sizes is tested using a *t* test conducted with R statistical software, version 2.2.1 (R Development Core Team, 2005). Boxplots are also employed to present the results graphically.

A total of 486 *C. granatina* shells were identified from this sample consisting of the following: 135 whole shells (27.8%), 232 broken shells (47.7%) from which measurements from shell parts were derived, and a remaining 119 shells (24.5%) for which no metrical observations could be established. In the case of *S. granularis*, a total of 521 shells were recovered from the same sample: 240 were whole shells (46.0%), 172 were broken shells (33.0%) but suitable for obtaining additional metrical data, and 109 shells (21%) for which no metrical data could be established.

Fig. 2 shows the boxplots for *C. granatina* and *S. granularis* shells analyzed for our case study. A *t* test revealed that the mean size of whole *C. granatina* shells (49.5 mm) is significantly smaller (*t* = 2.62, df = 239.3, *p* < 0.009) than that established from broken shells (52.7 mm). The overall mean based on whole and broken shells falls, and predictably so, in between these two values at 51.6 mm. Similarly, the mean size of whole *S. granularis* shells (33.3 mm) is also significantly smaller (*t* = 3.28, df = 370.8, *p* < 0.001) than that for broken shells (34.5 mm) of the same species, with an overall mean size pooling whole and broken shells together at 33.8 mm.

### 4. Discussion and conclusions

The most straightforward way to estimate limpet shell sizes from fragmentary material is to obtain measurements on inner length and/or inner width and on two or three other shell parts (total width, anterior and posterior lengths) that have the highest survival rate in archaeological contexts. These are likely to be the most abundant measurable shell parts for both of these limpet species in excavated samples. These measures can be combined with those obtained from any whole limpets that might be recovered in order to calculate overall mean sizes. In very highly fragmented samples with no whole limpets and/or low recovery of inner length and/or inner width, other measures employed in this analysis can also be used to estimate shell lengths (Fig. 1: LW, AL, PL). However, the use of peripheral shell parts based on the ventral side of the shell (Fig. 1: LIW, AIL, PIL) could increase the chances of two or more fragments of the same shell being measured. Careful selection and comparison of such marginal parts will be necessary, including refitting if needed. This will inevitably increase the time and costs of the analysis.

The use of morphometric equations holds three clear advantages. First and foremost they open up possibilities for obtaining shell-size data from severely fragmented samples that are too small to render statistically valid sets of limpet...
lengths. This is a pernicious problem for those studying the MSA exploitation of South African marine resources (Klein et al., 2004; Marean et al., 2004; Parkington, 2003; Steele and Klein, 2005). The results of our case study shows that the sample size of shell length measurements can be increased almost three fold for C. granatina and nearly two fold for S. granularis. These values can vary from case to case and are bound to be much higher where fragmentation, resulting from a combination of taphonomic factors, is more extensive than the one observed here. The second obvious advantage afforded by these equations is that they render it unnecessary to excavate large bulk shell samples in order to obtain enough whole limpets to conduct statistically valid analyses. The savings here are not only in recovery costs but also in transport, processing, storage space, and long-term curation costs.

A third contribution from the use of these equations is the possibility of basing calculations of limpet mean sizes on larger sample sizes and checking for possible preservation biases in the archaeological record. The statistically significant differences between mean sizes based on whole and fragmented shells show that fragmentation has mainly affected the integrity of larger shells and less so that of smaller shells in this specific case. The particular set of taphonomic factors that operated during and after the accumulation of GFG open air shell midden clearly biased the preservation of C. granatina and S. granularis shells, with smaller shells preserving better than the bigger ones. It is possible that the relatively larger surface area of bigger shells rendered these more susceptible to breakage due to trampling and other attritional factors when compared to smaller ones. Many of the latter were probably protected under larger shells and other gaps. These results of differential preservation may be repeated at other shell middens. However, a different combination of taphonomic factors (e.g., more protection from the elements offered by cave sites, different admixture of archaeological remains, different accumulation rates and varying degrees of burning, acidity and trampling) might well throw other results. These could range from minimum to maximum differential preservation, and/or preservation bias with an opposite trend to the one reported here. Consequently, the analyses and comparisons done here ought to be repeated with shell samples of the same and other limpet species and from an array of depositional contexts before the problem of differential preservation of southern African limpet shells in archaeological sites is properly understood.

The results presented here exemplify the power that morphometric equations have in complementing and enhancing measurements based solely on whole shells. Although the use and strength of morphometric equations has already been recognized and applied to archaeological reconstructions along the southern Pacific coast (Jerardino et al., 1992; Oliva and Castilla, 1992), the generation of these equations for other species elsewhere in the world would be of great benefit given the regular use of metrical observations on whole shells in archaeological reconstructions (Erlandson et al., 2004; Mannino and Thomas, 2002; Milner et al., 2007). Finally, the use of morphometric equations should not be restricted to new research cases only. These ought to be applied to re-evaluate inferred scenarios where whole shells have been the primary source of data.

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