Cape rock lobster (*Jasus lalandii*) exploitation in the past: estimating carapace length from mandible sizes

A. Jerardino[a*], R. Navarro[b] and P. Nilssen[c]

Morphometric equations for estimating carapace lengths of Cape rock lobsters (*Jasus lalandii*) were derived from mandible measurements for the purpose of zooarchaeological reconstructions. A linear regression model was based on measurements of males, females and both sexes combined, and for left and right mandibles separately. Statistically significant differences were observed between male and female regression slopes for left and right mandibles, and also between the slopes of left and right mandibles within each sex. The morphometric equations for males and females combined should be used when dealing with archaeological samples. These equations are also potentially useful research tools for marine biologists and conservationists involved in monitoring illegal exploitation of Cape rock lobsters.

Background

The study of animal remains from archaeological sites is a well-established field of enquiry, and is commonly known as zooarchaeology or archaeozoology. Its goal is to reconstruct the environment, behaviour and diet of people in the past by using observations based on bones, mollusc shells, crustacean and other faunal remains.[1–8] Shell middens are a principal source of suitable faunal material and have been the focus of basic quantitative analysis since the nineteenth century.[9,10] Although measurements of specimens sizes were used in earlier studies, metric analysis gradually has become standard archaeological practice over the last three decades.[1,3,6,9] An important motivation for taking such measurements is the reconstruction of body sizes and meat-weights (biomass) of animals collected by people in the past.

Because faunal material from archaeological sites is usually very fragmented, measurements of whole specimens are seldom obtainable. Consequently, methods for reconstructing animal body sizes from fragmentary remains have been developed. Morphometric equations are central to these procedures in that they allow valid estimates of body size and body biomass from measurements of skeletal parts and/or morphological features.[6,11–16] In South Africa, morphometric equations for two species of marine mussels were generated,[17,18] and both equations have been used by archaeologists.[19,20]

Along with several shellfish and vertebrate species, the Cape rock lobster (*Jasus lalandii*) was an important marine resource for people during the precolonial past along the Western Cape coast.[21–30] The presence of Cape rock lobsters in local archaeological sites is revealed by the preservation of their relatively hard, calcareous mandibles.[31] In fact, crustacean mandibles are the most reliable evidence for the exploitation of these taxa in archaeological sites around the world.[32–34]

Despite the recurrent appearance of Cape rock lobster mandibles in archaeological assemblages, little is known about the overall contribution of this resource to peoples' diet and the existence of possible changes in the exploitation of this species in the past. To answer such questions, a first priority is to obtain morphometric equations which relate the size of the left and right mandibles (as these are not identical) with carapace length measurements. Since the earliest systematic biological studies of this species,[35] carapace length has been used as a measure of the Cape rock lobster body size.

A first attempt to generate morphometric observations relating size measurements of Cape rock lobster mandibles with carapace length, total weight and tail weight was undertaken by Grindley.[31] The small number of observations, and the absence of mathematical equations that describe the morphometric relationship between these two variables, however, compromized this effort. Diagrams displaying best-fitted log curves were the only means by which this relationship was explored. Such diagrams are evidently not adequate for the accurate assessment of original animal size and/or body and tail mass on the basis of mandible size observations. Here, we present the required morphometric equations that relate mandible size with carapace length based on statistically adequate sample sizes and procedures.

Methods

Carapace length and size measurements of left and right mandibles were recorded in 1993, 1999 and 2000 from animals captured with traps off the west coast of South Africa by R. Melville-Smith and S. Mayfield. Measurements of mandibles and carapace lengths were obtained from fresh animals with a 0.05 cm precision calliper. Only one left mandible of a male specimen was not included in our data base. The mandible in question had grown abnormally after a healed fracture. Figure 1 shows the morphology of left and right mandibles and size measurements taken on them: 81 males with a range of carapace lengths from 46.9 to 131 mm and 61 females with a range of carapace lengths from 43 to 89 mm were measured. Biomass and edible meat weight of these animals were not recorded, as these specimens had to be returned for other research purposes.

Model I regressions[36] were conducted with a statistical program written by R. Navarro. It is important to note that Model I regressions work on the assumption that the independent variable (in our case, mandible size) is measured without error. Strictly speaking, this assumption is untenable, as human and instru-

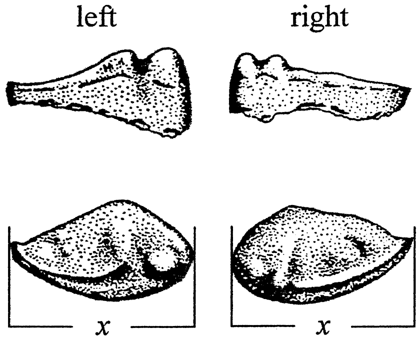

Fig. 1. Graphic representation of left and right mandibles (after Grindley[31]) of Cape rock lobster (*Jasus lalandii*) showing the measurements recorded.

[a]Department of Archaeology, University of Cape Town, Rondebosch, 7701 South Africa.

[b]Avian Demography Unit, Department of Statistical Sciences, University of Cape Town, Rondebosch, 7701 South Africa.

[c]Human Sciences Division, South African Museum, P.O. Box 61, Cape Town, 8000 South Africa.

*Author for correspondence. E-mail: chopi@beattie.uct.ac.za

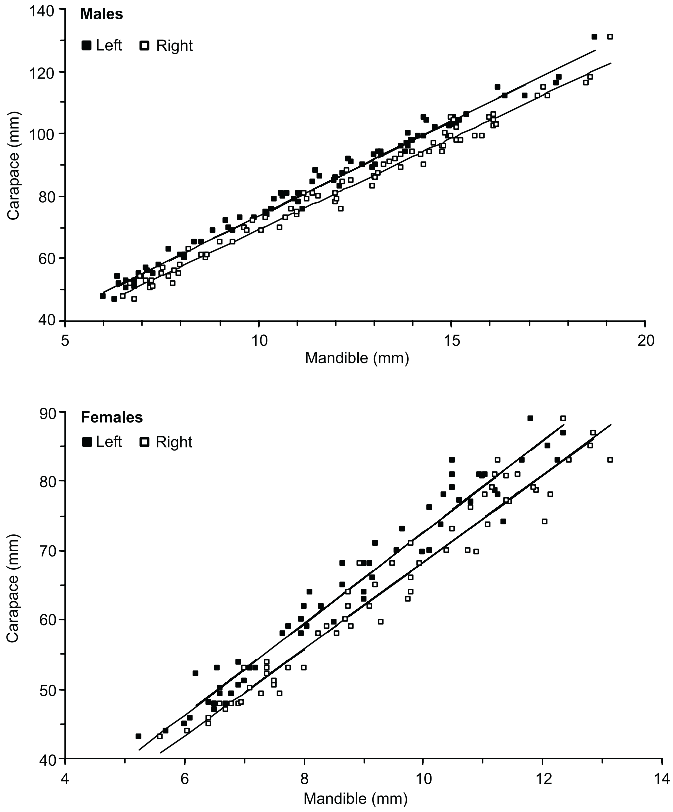

Fig. 2. Plots and regression lines of left and right mandible measurements according to carapace length for male and female Cape rock lobsters.

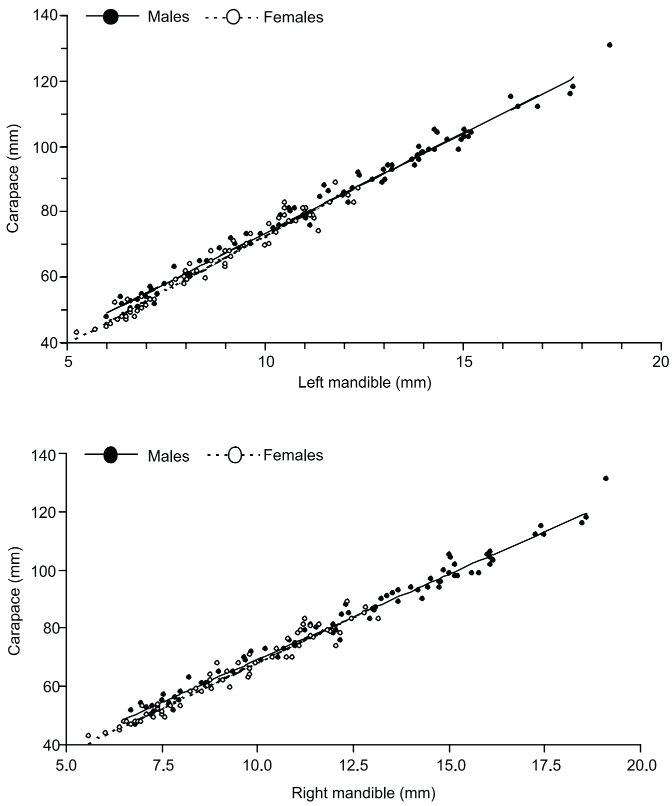

Fig. 3. Scatter plots and regression lines of male and female mandible measurements according to carapace length for left and right mandibles.

mental error cannot be eliminated when obtaining these or other measurements. Model II regression[36] is recommended for such cases. Unfortunately, the predictive power of Model II regressions is considerably less than that of Model I. Because the predictive power of morphometric equations is of crucial importance when applying them in archaeological cases, we opted for using Model I regressions while acknowledging that the use of this regression model violates one of the key assumptions, i.e. that the independent variable has been measured without error.

Model I regressions were conducted on three sets of data, namely i) males, ii) females, and iii) males and females combined. Analyses of covariance[36] (ANCOVAs) were performed to test differences in the slopes between male and female regression equations within each type of mandible, and between regression equations for left and right mandibles within each sex.

Results

Figure 2a, b shows the plotting of left and right mandible measurements according to carapace length for male and female Cape rock lobsters, respectively. As noticed by Grindley[31] and others, the size of right mandibles is consistently larger than that of left mandibles along the range of carapace lengths in both sexes. The mean difference between right and left mandible sizes for male specimens is 0.99 mm, and that between right and left mandible sizes for female specimens is 0.63 mm.

Table 1 presents the parameters (a and b) and coefficient of determination (r^2) of morphometric equations for the estimation of carapace length from size measurements on left and right mandibles. A linear regression model ($y = a + bx$) fitted the data best. The intercept for male equations is greater than that for female equations. The same is true when the intercepts for left mandible equations are compared to those of right mandible equations. The coefficient of determination for each morphometric equation is very high, which underlines their good predictive power.

ANCOVA results show that the slopes of morphometric equations for left and right mandibles are significantly different (males: $F = 6.40$, d.f. = 1, 157, $P < 0.05$; females: $F = 7.67$, d.f. = 1, 118, $P < 0.02$). ANCOVA also detected significant differences between the slopes of male and female morphometric equations for left ($F = 6.29$, d.f. = 1, 137, $P<0.05$) and right mandibles ($F = 7.60$, d.f. = 1, 138, $P<0.02$).

Figure 3 shows scatter plots with best-fitting lines (males and females) for left and right mandibles. In these graphs, and as also shown by the ANCOVA results, the slopes of male and female equations are clearly different. For a given mandible measurement within the small size range, females have smaller carapace lengths than males. Although almost no observations on female individuals are available for the upper size range, according to the slope trend it is reasonable to expect that female carapace lengths would be slightly larger than those of males within the

Table 1. Parameters of morphometric equations for the estimation of carapace length (males and females) from measurements on mandible sizes of Cape rock lobsters. The model used is that of a linear regression ($y = a + bx$), and measurements are in millimetres.

	Left mandible	Right mandible
Male	a = 12.34	a = 10.51
	b = 6.11	b = 5.86
	r^2 = 0.98	r^2 = 0.98
Female	a = 6.70	a = 5.64
	b = 6.59	b = 6.26
	r^2 = 0.96	r^2 = 0.95
Joint	a = 9.83	a = 8.44
	b = 6.29	b = 6.01
	r^2 = 0.98	r^2 = 0.97

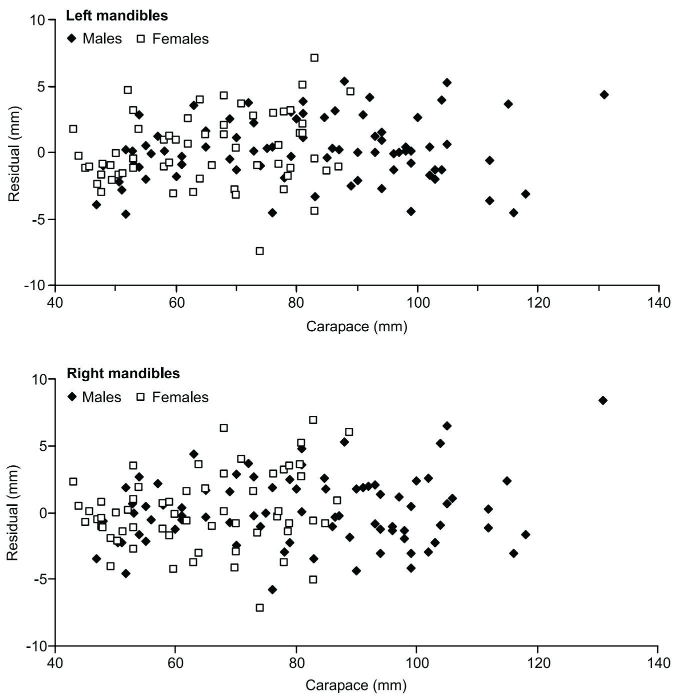

Fig. 4. Residual scatter plots of predicted carapace lengths from male and female equations for left and right mandibles.

larger mandible size range.

Figure 4 shows residual scatter plots of predicted carapace lengths from male and female equations for left and right mandibles. The residuals are homogeneously distributed around the estimated value (0), showing the adequacy of the linear regression model in each instance.

Figure 5 shows the male and female residuals of predicted carapace lengths using the joint (male and females together) equation for left and right mandibles. The homogeneous distribution of the residuals around the estimated value (calculated according to the joint equation) supports the use of this equation when dealing with a mixed set of mandible measurements from male and female Cape rock lobster specimens.

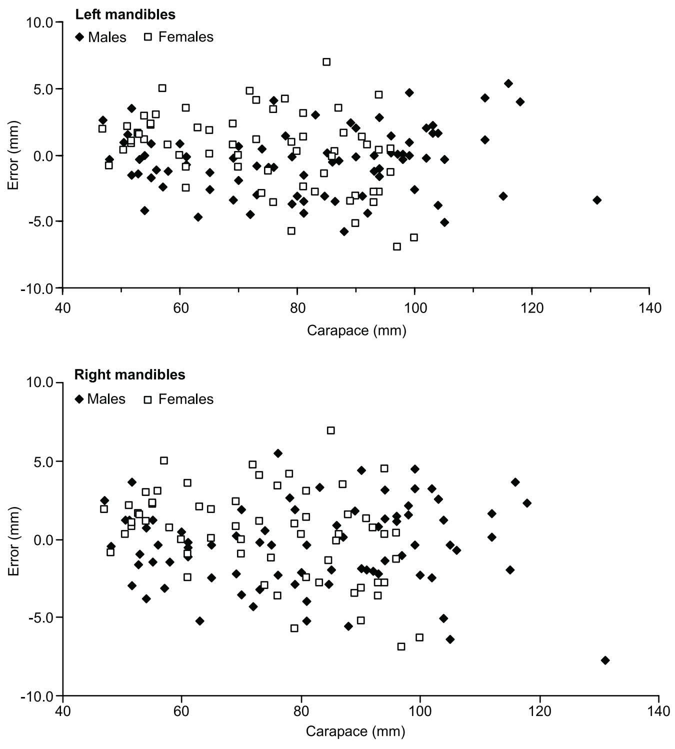

Fig. 5. Residual scatter plots of predicted carapace lengths using the joint equation for left and right mandibles.

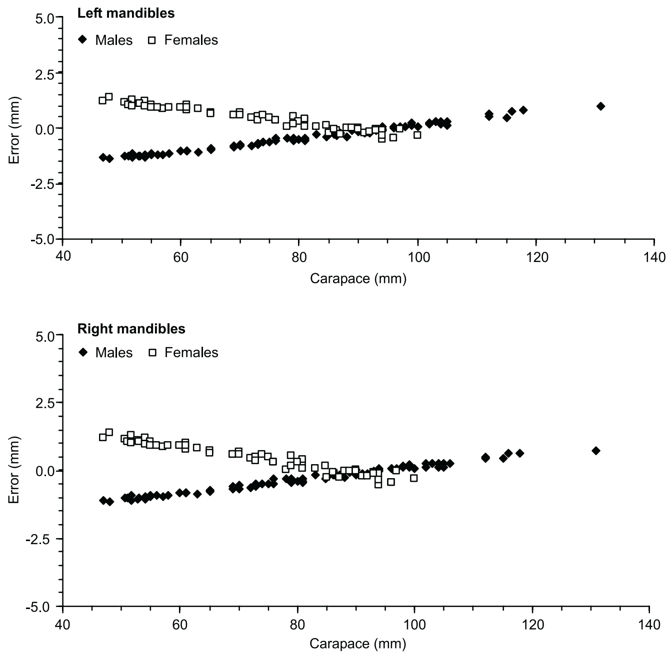

Fig. 6. Scatter plots of the difference between the predicted error calculated with joint equation and the predicted error calculated with either male or female equations, for left and right mandibles.

Figure 6 shows scatter plots of the difference between the predicted error calculated with the joint equation and the predicted error calculated with either male or female equations, for left and right mandibles. For both mandibles, the difference between these two errors is not constant along the range of carapace length. This difference increases for males and decreases for females along the range of carapace length. This shows that by using the joint equation, carapace lengths will be underestimated when measurements are based on male individuals or overestimated when measurements are derived from female individuals within the 45–100 mm carapace length range. This error, however, is small (between +2.0 mm and –3.5 mm in carapace length).

Discussion and conclusions

Mandible measurements of small individuals (43–53 mm carapace length) had to be undertaken with great care because of the fragility of the mandibles. Their delicate structure is probably the result of frequent, and perhaps also recent, moulting that characterizes juvenile lobsters.[37] The differential preservation of these small mandibles in archaeological contexts might inadvertently introduce a bias in the reconstruction of carapace size distributions, making intra- and inter-site comparisons difficult to evaluate. Consequently, it should be noticed that in cases where small mandibles are rare in archaeological samples, it might not necessarily reflect prehistoric peoples' selection for larger animals, but, instead, the poor preservation of small mandibles in some archaeological deposits.

The statistical results clearly show that carapace length estimations should be done according to sex and position of mandible. While position (left or right) of an archaeological mandible is easy to recognize from its overall morphological characteristics, there is no procedure by which it can be sexed. Consequently, the joint (male and female together) morphological equations for left and right mandibles should be used when dealing with archaeological mandibles. With the joint equation, however, the sizes of male specimens will be slightly underestimated and those of female specimens will be marginally overestimated within the small size range. These distortions in the estimates of carapace lengths would be minimized when dealing with large sample sizes, where male and female specimens are assumed to appear in roughly equal numbers. Although large samples of Cape rock lobster mandibles are not hard to find in archaeological contexts,[22,24,31,38] the assumption that any given archaeological sample would include males and females in roughly equal numbers is difficult to sustain. Access to Cape rock lobsters by precolonial coastal dwellers was most probably restricted to the low intertidal and shallow subtidal. Recently recorded natural walk-outs of Cape rock lobsters in Elands Bay consisted almost entirely of females,[39] most of which had originated from the nearby subtidal and low intertidal rocky reefs. Equal representation of male and female individuals in large samples is thus not guaranteed.

The morphometric equations presented here are not only valuable to archaeologists working at the coast, but also to those concerned with the illegal exploitation of Cape rock lobsters. These equations can prove useful in the reconstruction of original carapace sizes from the remains of poached lobsters. Direct measurement of the surviving carapaces is frequently impossible as these are often found brittle, sun-bleached and broken up. In such cases, as with archaeological examples, the hard, calcareous mandibles are the only surviving body parts that can provide clues about the original sizes of illegally captured lobsters.

The development and use of these particular morphometric equations will also allow the comparison of Cape rock lobster exploitation in the precolonial past with that undertaken today by the commercial and sport fisheries.[40,41] By contrasting the archaeological observations with those from monitoring programmes and recent catches from varying environmental settings, archaeologists will be better positioned to interpret the observed changes in the archaeological record.

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