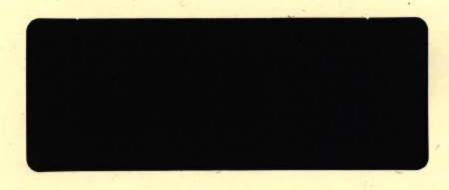
TUHINGA

Records of the Museum of New Zealand Te Papa Tongarewa

The estimation of live fish size from archaeological cranial bones of the New Zealand barracouta *Thyrsites atun*

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The estimation of live fish size from archaeological cranial bones of the New Zealand barracouta *Thyrsites atun*

B.F. Leach¹, J.M. Davidson¹, L.M. Horwood² and A.J. Anderson³

ABSTRACT: Twenty-four measurements were taken on five of the paired cranial bones and the otoliths of a modern sample of 278 barracouta, *Thyrsites atun*. Regression analysis was performed on these measurements to estimate live fork length and ungutted weight. A number of regression models were examined (linear, logarithmic and power curve) to work out the optimum estimator for each bone measurement. It was found that live fork length of this species can be estimated with a standard error of less than \pm 46 mm, and the weight to less than \pm 390 g. Coefficients are provided for 48 equations linking bone size to live characteristics. This is followed by a study of barracouta from an archaeological site at Long Beach, Otago. Measurements were made on 15,558 archaeological bones with a Minimum Number of Individuals of 4,505. It was found that the barracouta catch had near normal characteristics with a mean fork length of 795 mm and SD of 51 mm. The mean body weight was estimated at 2347 g. The usable meat weight represented by these fish is estimated to be 7.4 metric tonnes.

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INTRODUCTION

The New Zealand barracouta, *Thyrsites atun*, is present in many archaeological sites in New Zealand. These fish are widespread and common around New Zealand although they are generally more abundant about and south of Cook Strait. They swim in schools, are voracious surface-feeding carnivores and are easily caught on a trolling lure. In the past Māori often caught them by jigging with a feather- and/or shell-decorated lure or even a plain piece of wood with a bone hook inserted through it. Early commercial fishermen also jig-fished surface-feeding barracouta using a piece of red wood with a nail driven through it on a short line (Graham 1974: 310ff.).

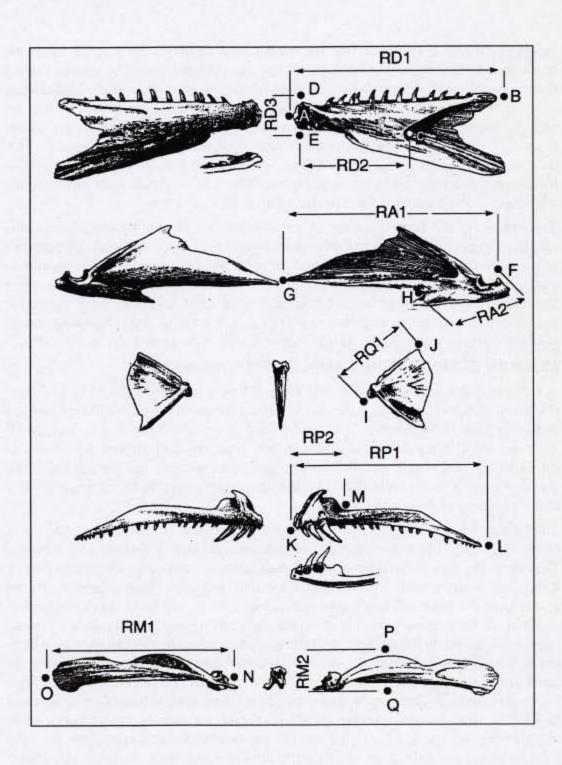
Today, barracouta are becoming an increasingly valuable commercial species. The size-frequency curve of fish catches is basic to the examination of issues such as the possible impact of fishermen on inshore fish stocks and changes in fishing technology over time. The weight of fish represented by a catch is primary information for studies of prehistoric economy. Because the species was prominent in some pre-European Māori fish catches it is desirable to have a well developed technique for estimating the live fish size and weight from archaeological bones. This is the focus of this paper.

BONE MEASUREMENT METHODOLOGY

The bones used for measurement are the otoliths and five paired cranial bones, the dentary, articular, quadrate, premaxilla, and maxilla. These bones have been used for many years to quantify prehistoric fish catches from archaeological sites in the Pacific and New Zealand (Leach and Davidson, 1977; Leach and Ward, 1981; Leach, 1986; Leach and Boocock, 1993). They do not always survive intact in barracouta; therefore it is desirable to include measurements which are applicable to incomplete bones. For this reason more than one measurement was made on four of the five bones involved. Whenever possible the largest dimension is always taken, as this yields the most reliable estimate of the original fish size. Thus, there are a series of measurements appropriate to whole bones and another series appropriate to various forms of bone fragment. The dimensions chosen are illustrated in Figure 1. These closely parallel those employed by archaeozoologists on other species (Rosello-Izquierdo, 1986:35; Libois and Libois 1988; Sternberg, 1992; Wheeler and Jones, 1989:139 ff.).

The anatomical landmarks used in this study are indicated on Figure 1 by a small dot and given a letter code from A to S. Each measurement was given a computer code with three characters. Thus, LD1 refers to the Left Dentary and the first measurement made on that bone. In cases where the terminology 'maximum length' or 'maximum

Figure 1: Cranial elements of *Thyrsites atun* (barracouta) used for measurements. The right bones are illustrated. Measurements are made between landmarks A-B, A-C, and D-E on the dentary; between F-G and F-H on the articular; between I-J on the quadrate; between K-L and K-M on the premaxilla; between N-O and P-Q on the maxilla; and between R-S on the otolith.



height' is used, this implies that the measuring callipers were rotated about the nominated landmarks until a maximum value was obtained. It will be seen in Table 1 that fragment measurements were not taken for the quadrate and otolith. The number of these bones identified for any one species is generally considerably lower than for other bones, and in particularly large assemblages the quadrate is sometimes excluded from the analysis, because of difficulties distinguishing between some species. Furthermore, the quadrate and the otolith are quite robust and an adequate sample of measurements can be taken on whole bones. Three measurements are indicated for dentaries, and two each for the articular, premaxilla and maxilla.

The purpose of the three character code is to permit simple coding of measurements on plastic bags containing identified archaeological fish bones. These are later entered into a database according to the original archaeological provenance. The appropriate equation for estimating live fork length and weight is selected using these three character codes. Mitutoyo digital callipers model 500-322 were used for linear measurements which are recorded to \pm 0.01 mm precision, and a Sartorius model BA310S balance was used for weight measurements with a precision of \pm 0.001 g.

MODERN COMPARATIVE SAMPLE OF Thyrsites atun

A sample of 278 fish was used in this study; 33 were obtained from MAF Fisheries (Ministry of Agriculture and Fisheries) in 1989, a further 200 from Seafresh Fisheries at Lower Hutt in September 1992, and a final group of 45 specimens from MAF Fisheries trawled in February and March 1993 from south of Stewart Island. It was difficult obtaining very large specimens of barracouta to ensure that the full size range was represented in the collection. The fish in the last group of 45 were specifically chosen because of their large size.

The first group of 33 specimens from MAF was obtained in Wellington and sent to Otago University whole for weighing, measuring and extraction of the cranial bones. This work was done in collaboration with staff in the Anthropology Department there. This initial study revealed how important it is to pay very close attention to exact definitions of anatomical landmarks and measurements, including the orientation of callipers. At the start of the next phase of the study, the measuring procedure was more thoroughly tested. In this respect, multiple re-measurement of specimens using different operators was particularly instructive. We also carried out experiments with the same operator measuring the same bones up to five times without knowledge of prior results in each case. Once again, this showed the importance of careful definition and familiarity with calliper orientation. Measurements of archaeological bones from several sites taken during the initial study had to be abandoned for two reasons - the final measurement definitions were slightly different than those initially formulated, and a number of errors were found during repeat measurements. The sample from Long Beach was therefore completely re-measured (see below), but those from other sites will need to be re-measured at some future time.

When full confidence was obtained in the measurement procedure, larger samples of modern barracouta were then processed. Specimens from Seafresh Fisheries were weighed and the fork length measured at the factory, after which the heads were removed for later processing at the Archaeozoology Laboratory at the Museum of New Zealand. In the third sample, the fork lengths were measured at sea, and the heads removed and frozen for later processing. Weight measurements were not taken at sea. The relationship between barracouta fork length and body weight has been intensively studied by fisheries scientists (Hurst 1988, Hurst and Bagley 1987, Hurst *et al.*, 1990). For this southern sample, weights were estimated using the equation published by Hurst *et al.* (1990: 35), namely weight = 0.009*fork length^{2.86}. This formula relates to combined males, females and juveniles in the region of southern Stewart Island and the Snares Island area, and therefore seems the most appropriate. The cranial bones of these fish were prepared in the Archaeozoological Laboratory during 1994.

The complete sample of 278 fish had fork lengths ranging from 460 to 885 mm with a mean of 693 mm. The ungutted weights ranged from 460 to 3538 g with a mean of 1555 g. Information was collated for 26 variables, consisting of fork length, ungutted body weight (with the exception of the second MAF sample), and 24 bone measurements. Some bones were broken or missing (many of the otoliths were not retrieved), and therefore not all measurements were able to be taken. The final data matrix of 7,228 entries had 598 missing values (Table 1). In cases where pairs of variables were being used for covariance calculations, arrays were concatenated by deletion of examples with missing values.

It will be seen in Table 1 that two measurements stand out as having a sizeable number of missing values. These are the lengths for the articular and premaxilla. About 12% of these measurements could not be taken because small parts of the bones were broken during processing. Archaeological bones might be expected to suffer even more damage than this. This is borne out by a study of barracouta bones from the site of Long Beach near Dunedin. Measurements were made on 15,559 bones, as shown in Table 1. Although this demonstrates how important it is to measure bone fragments, it must be remembered that if bones are complete the maximum measurement should always be taken as this is the most reliable estimator of original fish size. Otoliths were not retrieved in the Long Beach excavation, which explains why no otolith measurements are listed in Table 1.

LEAST-SQUARES ANALYSIS OF MODERN COMPARATIVE MATERIAL

The main objective of this study was to establish reliable regression relationships between bone dimension and live fork length and ungutted weight which can then be used for studying archaeological bones. To this end, regression analysis was carried out on the measurements of the osteological collection taking each bone dimension individually, and testing various types of curve fitting procedures to the data using the

least-squares method. The general equations for estimating Y from X are as follows (A = constant, B = slope):

Linear Fit Y = A + B * XExponential Fit Y = A * exp(B * X)Logarithmic Fit Y = A + B * In(X)Power Curve Fit Y = A * X * BCubic Fit Y = A + B * X * 3

The various curve fitting procedures are shown in Figure 2 using the example of the right dentary length. The statistics for the regression analysis estimating live fork length and ungutted weight from the left dentary length are given in Table 2.

Inspection of this Table will reveal that in estimation of both fork length and weight, the best model is that of the power curve fit. This is evident in the values for the correlation coefficient, the standard error of the estimate, and the residuals. The fact that all three statistics show this is not really surprising since they contain similar terms. When the various models are graphed as regression lines, along with plots of the original data points, it becomes abundantly clear that not all models are very appropriate. For example, in the case of estimating fork length from bone dimension, the logarithmic and cubic functions do not conform to the scatter of data points at all, and this is reflected in very large residuals in Table 2. By contrast, the exponential, linear and power curve fits all appear to model the data quite well, and one is hard pressed, simply from Figure 2, to decide which model is best. The standard error of the estimate was used in all cases to make such decisions, choosing the lowest value, which in this case is ± 22.3 mm. Thus, in Table 3, where the choices of model are summarised, the power curve fit is entered, along with the appropriate regression constants, as the best means of estimating fork length from measurements of the left dentary.

The same procedure is followed for estimating the live fish weight. In Figure 2 it will be seen that when the left dentary length is plotted out against weight, only three of the regression models appear at all suitable. In this case, it is the linear and logarithmic models which can be rejected. The remaining three, once again, are rather difficult to separate. However, in Table 2 it can be seen that the values for the correlation coefficient, standard error of the estimate, and residuals, are all lowest for the power curve fit. Consequently, these values are entered into Table 4.

Figure 3 shows the final two choices of regression model for the left dentary length, with all fish in the comparative collection plotted against the regression curves with 95% confidence bands. The two solutions are very satisfactory.

This selection method was followed for all 24 measurements, enabling best fit regression equations to be chosen, and thereby completing the tabulations given in Tables 3 and 4. In Figure 4 and 5 the best and worst fits are illustrated for estimating fork length and weight respectively. The otolith measurements in both cases give the worst results. This is partly due to the much smaller sample size in the case of otoliths (see Table 1). The range of errors associated with the final choice of regression models is illustrated in Figure 6. Fork length errors range from \pm 21 to 51 mm, and weight errors range from \pm 226 to 381 g. These are very reasonable.

It is useful to follow a worked example. For this purpose, a modern fish of medium size in the comparative collection was chosen, catalogued as specimen AA866. This fish had a live fork length of 610 mm, and an ungutted weight of 1010 g. The left dentary length LD1 was 54.32 mm.

From Table 3 it will be seen that the best fit model for estimating fork length from the LD1 bone measurement was found to be a power curve fit, and this can be extracted from the Table as follows:

Fork Length mm =
$$14.66816 * LD1^{0.9281766} \pm 22.3$$

In Table 4 it will be observed that the best fit model for estimating live weight from the LD1 bone measurement was also found to be a power curve fit, and this can be extracted from the Table as follows:

Weight
$$g = 0.01180962 * LD1^{2.823251} \pm 231.4 g$$

By substituting the value of LD1 of 54.32 into these two equations, we derive estimates for the fork length of 598 mm, and for weight of 934 g. The error in estimating the fork length is therefore 12 mm (610-598), and in estimating the weight 76 g (1010-934).

There are two methods by which an estimate can be obtained of the original weight of the fish. One could work directly from the bone to the weight, using the comparative material assembled for this present study, or one could adopt a two-step process; firstly estimating the fork length from the bone dimension, and then secondly estimating the weight from the fork length. There is a potential shortcoming in the first approach, in that this present osteological sample of 278 fish is relatively small and does not contain many very small or very large specimens. Thus, with archaeological material we may sometimes be obliged to extrapolate beyond the size limits of the osteological collection. This is not a serious problem in the case of regression equations which are close to linear; however, it could produce significant errors when a regression relationship

close to a cubic function. Fortunately, MAF Fisheries scientists have studied the relationship between fork length and body weight for very large samples of fish, and also for different sexes, at different seasons, and at different localities. As mentioned above, in this present study we used the equation published by Hurst *et al.* (1990: 35), notably:

weight = 0.009* fork length $^{2.86}$

One way of trying to evaluate the relative merits of these two approaches is to examine the residuals, that is, the difference between observed and estimated fork length and weight, using estimates from the two models. This was carried out, and the results are graphed in Figure 7. The mean of the residuals is close to zero for estimates of fork length and for the one-step weight model, but for the two-step weight model it is -15.6%, which seems rather large. Moreover, the range of residuals is rather larger in the case of the two-step model. Despite this apparent advantage of the one-step model, it is suggested that in cases where archaeological bones are either very small or very large, the two-step procedure is the preferable model to use. The dangers of extrapolation are well known.

PUTTING THE ALGORITHMS TO WORK

Following the identification of anatomy and species of archaeological fish bone collections, wherever possible one, and only one, of the bone dimensions described in Table 1 is measured on each bone. The measurements are then entered into a computer file by provenance and bone code. As an example of the procedure, we chose measurements we have made of bones from the site at Long Beach, Otago (Hamel and H.M. Leach 1989, and H.M. Leach and Hamel 1981). A typical selection of coded measurements from this site appears below:

Long Beach Site Barracouta Archaeological Measurements

LOBE023 Layer 9

LD2 40.15 42.99 43.33 46.62 39.56 42.52 42.09 41.51 40.37 40.91 40.90 39.85

LD1 83.45 77.92 78.38

LD3 08.30 10.02 11.39 10.18 09.67 09.89 11.65 10.67 10.15 08.84

RD2 39.87 41.13 42.37 41.00 45.59 39.42 46.92 40.17 39.65 44.14

RD1 73.83 73.37 70.08

RD3 10.70 10.03 09.68 09.03 10.94 09.98 11.51 09.23 09.46 10.26 10.15 09.20

Of the 34,035 fish bones identified to species at this site (Leach and Boocock, 1993: 121), we were able to measure 15,558 bones from barracouta, which has an MNI of 4,505 fish. Thus, we measured 3.45 times the number of barracouta MNI. This may initially appear a somewhat strange approach to obtainining a size-frequency distribution of the original fish catch. For example, an alternative might be to take one measurement on the most numerous bone in the collection. In this way the number of measurements taken would be the same as the MNI. However, it should be remembered that the MNI represents only the *minimum* number of individuals in the site, and since our technique of obtaining the MNI does not take into account bones which are mis-matched by size, measurements taken only on the most numerous bone may produce a biased size-frequency histogram.

This issue has been the subject of formal theoretical analysis by Leach and Boocock (1995: Appendix 1) using a computer simulation model. This involved taking a large sample of bones from a fish catch where the size-frequency diagram and associated dispersion statistics were known, and carrying out recursive simulated breakage of bones so they could not be measured. It was concluded that estimating the size-frequency distribution on the basis of all possible measurements did not produce bias. This approach was therefore adopted in this present study.

With the aid of a simple computer program, the 15,558 barracouta bone measurements were converted into estimates of fork length using the coefficients listed in Table 3, and into estimates of ungutted weight, using the two-step model referred to above. The resulting histogram of fish length is illustrated in Figure 8, together with the dispersion statistics. The histogram displays near normal characteristics, with very slight negative skewness and positive kurtosis (g1 and g2 depart from 0.0 and 3.0 respectively). Although this non-normality is only slight, the W statistics show both g1 and g2 values to be significant.

The mean weight of the fish represented by these bones was estimated to be $2,347 \pm 3.8$ g (that is, $\pm 0.016\%$). From this, we can calculate the total weight of barracouta, using the MNI value (Minimum Number of Individuals) published by Leach and Boocock (1993: 197–207). Of the total MNI of 5,770 fish at this site, 4,505 were barracouta (78.1 %). Thus, the total weight of barracouta can be calculated as:

Mean Body Weight x MNI Total Body Weight Usable Meat Weight 2347 g x $4505 = 10,575 \pm 7 \text{ kg}$ 7,402 kg

Smith (1985: 487-488) recommends using a figure of 70 % for the amount of usable meat weight per total body weight for the common species of New Zealand fishes. At Long Beach, this is therefore estimated to be about 7.4 metric tonnes of barracouta

meat. The stated error of \pm 7 kg for the total body weight is based on the standard error of the mean weight of fish, which is \pm 0.016%.

CONCLUSIONS

This study was aimed at finding the most reliable means of estimating live fork length and ungutted weight of the New Zealand barracouta, *Thyrsites atun*, from bones and bone fragments. Using a modern sample of 278 fish, it was established that live fork length of this species can be estimated with a standard error of less than \pm 46 mm and weight with a standard error of less than 390 g.

Two methods of estimating live weight were explored: a one-step method directly from the bone to the weight, and a two step method, estimating fork length from bone measurement, and then estimating weight from fork length. Although results using the one step method on this sample seemed more satisfactory, it is suggested that the two step method should be used when archaeological bones are either very large or very small.

The ultimate aim of this study is, of course, to improve understanding of the nature of pre-European catches of barracouta. The methodology that had been developed was applied to 15,558 barracouta bones, with a Minimum Number of 4,505 Individuals, from an archaeological site at Long Beach, Otago. This barracouta catch had near normal characteristics. The mean fork length was 795 ± 51 mm, and the mean body weight 2347 ± 3.8 g. The usable meat weight represented by these fish was estimated to be 7.4 metric tonnes.

Application of the methodology to other archaeological remains of barracouta will enhance our understanding of past Māori use of this important resource.

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FIGURES

Figure 2: Several regression models were applied to the measurement of left dentary length and live fork length and weight (N=275). Note that some of the lines of best fit are difficult to distinguish—notably the power curve, exponential and cubic fits in the case of weight estimation, and power curve, exponential and linear fits in the case of fork length.

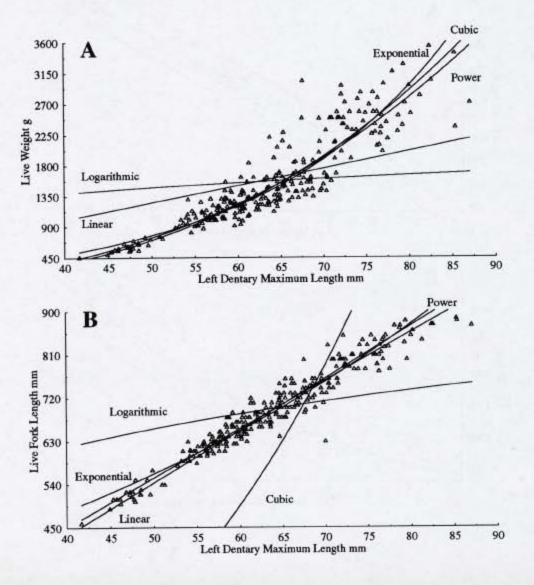


Figure 3: The regression model which best fits the data when estimating fork length (A) and ungutted weight (B) from the left dentary length is a power curve fit in both cases. The 95% confidence boundaries for the regression line of y on x are shown. The standard errors are \pm 22 mm for the fork length, and \pm 231 g for the weight. The powers are 0.92 and 2.82 for fork length and weight respectively. These values are close to linear and cubic.

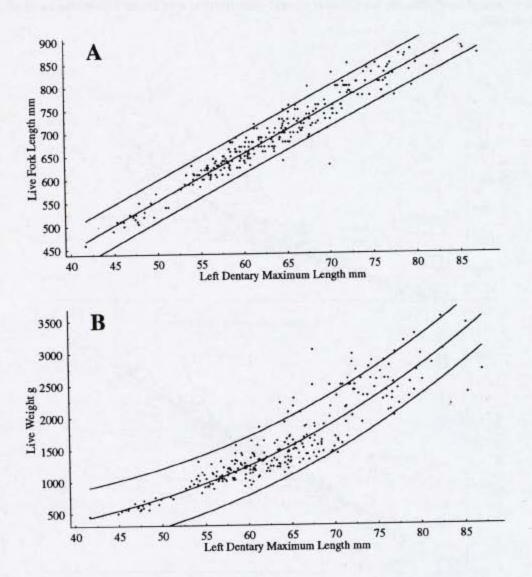


Figure 4: This shows the best (A) and the worst (B) fit regression lines for estimating fork length from bone measurements. The best measurement is the right articular length, which has a standard error of the estimate of \pm 21 mm; and the worst is the right otolith maximum length with \pm 51 mm.

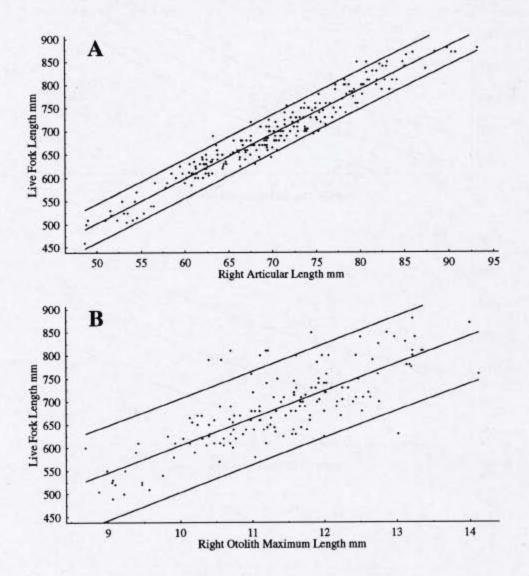
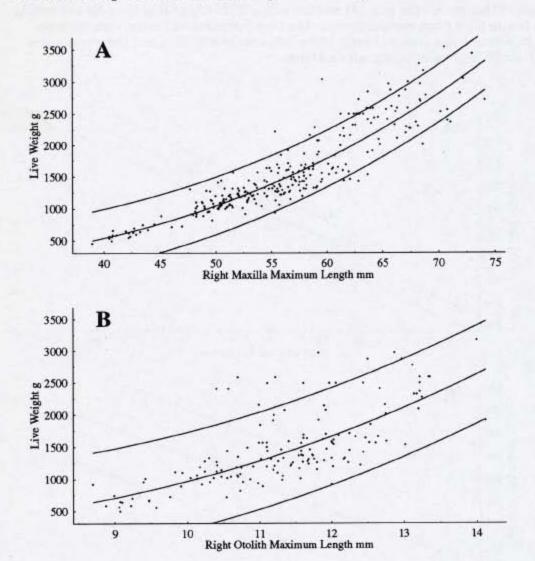
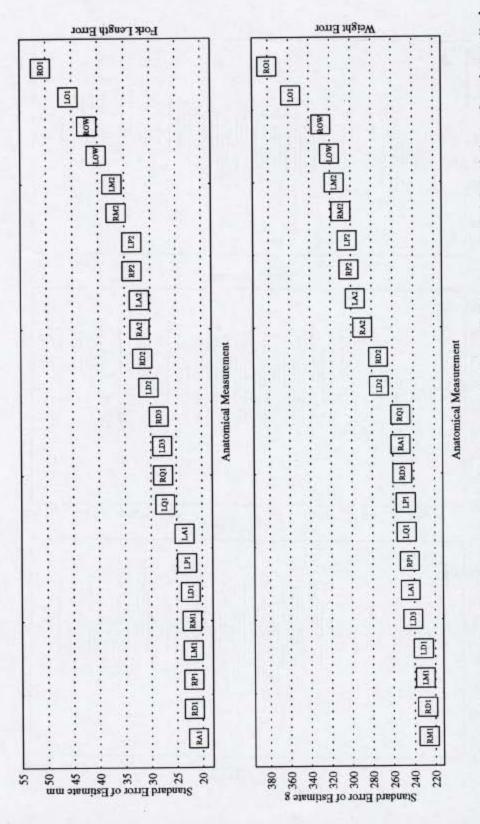


Figure 5: This shows the best (A) and the worst (B) fit regression lines for estimating ungutted weight from bone measurements. The best measurement is the right maxilla maximum length, which has a standard error of the estimate of \pm 226 g; and the worst is the right otolith maximum length with \pm 381 g.





errors is similar for any one measurement between the two graphs. Note that the comparatively poor performance of the Figure 6: These two graphs show the range of standard errors of the estimate for both fork length (upper) and ungutted weight (lower) for all bone measurements taken. These range from 21 to 51 mm and 226 to 381 g. The general pattern of otolith measurements is partly due to the low number of measurements made on these bones

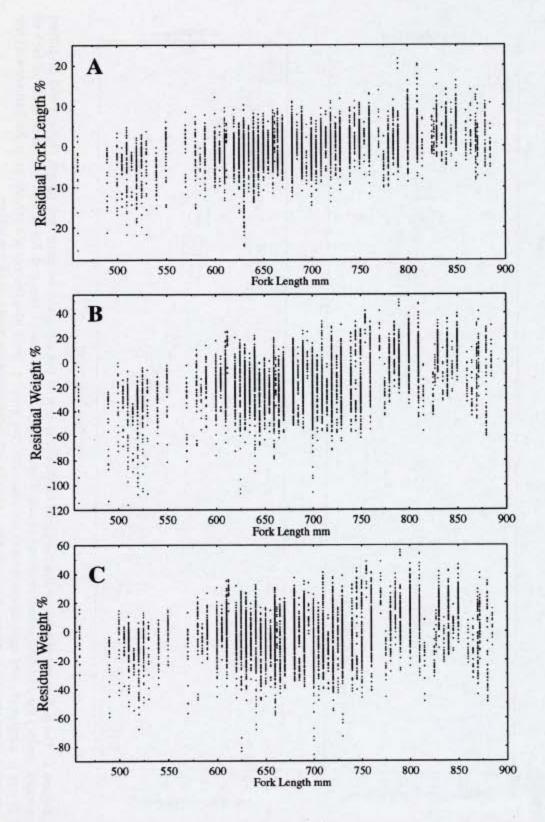


Figure 7 (left): Analysis of residuals of estimated and actual fork length (A), and weight using the two step-model (B) and one step model (C). The 278 fish in the comparative collection produced 7228 measurements which are used in this analysis. In A the range of residuals is -25.7 to 21.6 %, with a mean of -0.2 %. In B the range is -116.3 to 50.1 % with a mean of -15.6 %. In C the range is -85.7 to 56.4 % with a mean of -1.6 %. The two step model is preferred in cases of archaeological bones that are very small or very large.

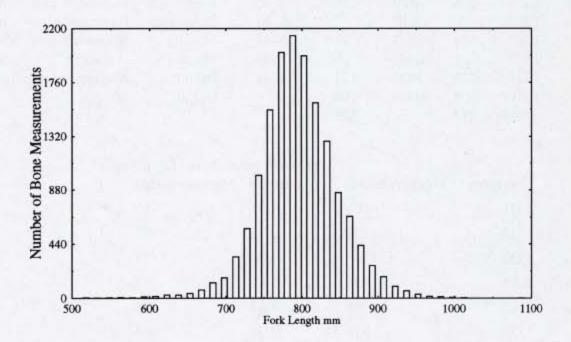


Figure 8: Size-frequency histogram of barracouta fork lengths from the Long Beach Site, Otago. This is based on 15,558 bone measurements. The fork length range is 503 to 1087 mm; with a mean of 795 \pm 0.4 mm; SD = 51.2 \pm 0.3 mm; g1/W1 = -0.03, 9.3; g2/W2 = 4.86, 47.4.

Table 1. Measurements made on cranial bones

Modern Comparative Collection							
Left	Missing	Right	Missing	Landmarks	Bone	Dimension	Units
LD1	4	RD1	3	А-В	Dentary	Length	mm
LD2	3	RD2	3	A-C	Dentary	Fragment 1	mm
LD3	2	RD3	1	D-E	Dentary	Fragment 2	mm
LA1	32	RA1	33	F-G	Articular	Length	mm
LA2	1	RA2	1	F-H	Articular	Fragment 1	mm
LQ1	1	RQ1	2	I–J	Quadrate	Maximum Len	gth mm
LP1	18	RP1	30	K-L	Premaxilla	Maximum Len	gth mm
LP2	0	RP2	0	K-M	Premaxilla	Fragment 1	mm
LM1	1	RM1	1	N-O	Maxilla	Maximum Len	gth mm
LM2	1	RM2	0	P-Q	Maxilla	Fragment 1	mm
LO1	122	RO1	123	R-S	Otolith	Maximum Len	gth mm
LOW	108	ROW	108	-	Otolith	Weight	g
Totals	293		305				

		Archaeological Bones Long beach		
Anatomy	Measurements	Anatomy	Measurements	
LD1	109	RD1	95	
LD2	1123	RD2	1085	
LD3	1763	RD3	1857	
LA1	38	RA1	13	
LA2	735	RA2	650	
LQ1	945	RQ1	866	
LP1	10	RP1	11	
LP2	2536	RP2	2523	
LM1	128	RM1	121	
LM2	489	RM2	462	
LO1	0	RO1	0	
LOW	0	ROW	0	
Totals	7876		7683	

Table 2. Least squares analysis of left dentary length with both fork length and live weight

Several regression models were applied to these data, and the results are presented below. In each case, it was assumed that the various curves passed through the origin.

A	=	regression constant
В	=	regression slope
R	=	correlation coefficient
SER	=	standard error of R
t	=	Student's t value for R
Residuals	=	sum of squared residuals
SEEy	=	standard error of estimate of fork length or weight

Live Fork Length mm SEE t Residuals Fit A B R SER 61.2 10.86753 23.1 .004 224 Linear 0.0 .966 24.9 .005 56.5 249 Exponential 269.9808 .01467313 .960 167.7702 23.1 .004 61.2 .966 1845 Logarithmic 0.0 22.3 63.4 Power Curve 14,66816 .968 .004 203 .9281766 .00229981 .943 29.5 .007 46.7 13470 Cubic 0.0 Live Weight g t Residuals B SEE SER Fit R A .897 282.2 25.10986 .012 33.5 38794 Linear 0.0 Exponential 82.66283 .04472431 .927 240.1 .009 40.6 11355 Logarithmic 378.448 .882 300.3 .013 30.9 67250 0.0

.932 231.4

.902 275.4

2.823251

.00563727

.01181

0.0

Power Curve

Cubic

42.4

34.5

10368

10733

.008

.011

Table 3. Best fit coefficients for fork length estimates

The coefficients given in this table are those for the equations which gave the lowest standard error of the estimate for all regression models tested. In each case it was assumed that the curves passed through the origin. Length dimensions are mm, and otolith weight are g.

Best Fit	Measurement	Constant	Slope	Standard Error
Power	LD1	14.66816	.9281766	22.3
Power	LD2	25.24488	.9254025	30.3
Logarithmic	LD3	0.0	340.5961	27.7
Power	LA1	12.23928	.9503028	23.4
Power	LA2	32.03885	.9506441	32.1
Power	LQ1	53.57143	.8510826	27.2
Power	LP1	12.26674	.9897375	23.0
Power	LP2	51.58221	.9396204	33.5
Power	LM1	15.25594	.9474989	21.7
Power	LM2	112.5328	.8418415	37.2
Power	LO1	48.70951	1.088216	45.6
Power	LOW	2849.963	.4792592	40.3
Power	RD1	14.51648	.9303367	21.6
Power	RD2	24.31129	.9351852	31.5
Logarithmic	RD3	0.0	340.5522	28.4
Linear	RA1	0.0	9.91286	20.9
Power	RA2	33.00574	.9409429	32.0
Power	RQ1	52.82623	.8566261	27.6
Power	RP1	12.15529	.9911504	21.7
Power	RP2	51.78013	.9381002	33.4
Power	RM1	14.42440	.9614360	22.0
Logarithmic	RM2	0.0	323.9209	36.4
Power	RO1	63.08101	.9818707	50.9
Power	ROW	2787.917	.4707007	42.0

Table 4. Best fit coefficients for weight estimates

The coefficients given in this table are those for the equations which gave the lowest standard error of the estimate for all regression models tested. In each case it was assumed that the curves passed through the origin. Bone dimensions are in mm, and the ungutted weights and standard errors are in g.

Best Fit	Measurement	Constant	Slope	Standard Error
Power	LD1	.01180962	2.823251	231.4
Power	LD2	.06235836	2.811234	273.0
Power	LD3	17.15709	2.166031	241.3
Power	LA1	.006613909	2.897941	243.5
Power	LA2	.1368774	2.869172	295.9
Power	LQ1	.55643	2.618509	247.2
Power	LP1	.007530183	2.986930	247.8
Power	LP2	.5840234	2.830956	303.4
Power	LM1	.01263143	2.895299	229.6
Power	LM2	5.937196	2.550728	315.8
Power	LO1	.5717217	3.215370	357.5
Power	LOW	102755.4	1.442137	320.0
Power	RD1	.01095188	2.840518	227.6
Power	RD2	.05129052	2.863828	273.6
Power	RD3	17.42051	2.158244	251.0
Power	RA1	.007017544	2.883040	252.4
Power	RA2	.1417015	2.856889	288.8
Power	RQ1	.5432451	2.628900	252.6
Power	RP1	.007140699	2.997758	244.3
Power	RP2	.5828517	2.831289	301.8
Power	RM1	.01059769	2.939167	226.2
Power	RM2	5.778976	2.566224	309.5
Power	RO1	1.045843	2.966582	380.6
Power	ROW	100192.5	1.429527	328.5

Appendix 1. Definition of measurements made on cranial bones

Abbreviation & Landmarks		Description
RD1 A-B	Dentary Maximum Length	The maximum length from the dentary symphysis to the most posterior margin of the dorsal transverse process.
RD2 A-C	Dentary Fragment 1	The length from the dentary symphysis to the anterior margin of the two transverse processes.
RD3 D-E	Dentary Fragment 2	The height of the dentary symphysis.
RA1 F-G	Articular Length	The length from the most superior point of the posterior border of the articular notch (F) to the most anterior point.
RA2 F-H	Articular Fragment 1	The length along the medial surface from the most superior point of the posterior border of the articular notch (F) to the anterior point of intersection of the transverse process and body.
RQ1 I-J	Quadrate Maximum Length	The maximum length from the most anterior lateral edge of the articulating surface to the most posterior point of the superior margin (rotate callipers).
RP1 K-L	Premaxilla Maximum Length	The maximum length (rotate callipers).
RP2 K-M	Premaxilla Fragment 1	The width from the most anterior part of the symphysial process to landmark M, which is the point of intersection between the transverse and vertical rami of the premaxilla.
RM1 N-O	Maxilla Maximum Length	The maximum length, excluding the small anterior spine (rotate callipers).
RM2 Q-P	Maxilla Fragment 1	The height of the anterior portion of the maxilla body.
RO1 R-S	Otolith Maximum Length	The maximum length (rotate callipers).
ROW	Otolith Weight	The weight.

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