

Using Allometry to Predict Body Mass from Linear Measurements of the White Shark

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Introduction

Morphometric proportions have been used by many authors in studies of morphology, taxonomy, and growth. Garrick (1960) reviewed changes in the proportional dimensions in sharks and reported qualitative features that various shark species have in common, including the observation that sharks showed accelerated growth (positive allometry) in the trunk compared to the head and tail. Clark and von Schmidt (1965) observed positive allometry for the trunk in a number of species belonging to disparate families. Bass (1973) and Bass *et al.* (1975) gave extensive quantitative summaries of proportional dimensions for sharks from the east coast of southern Africa, including complete morphometrics for white sharks *Carcharodon carcharias* of total length (TL) ranging from 1.70 to 3.91 m.

The linear size-on-size regression $y = a + bx$ has been used successfully as an aid to shark taxonomy (Steffens and D'Aubrey, 1967). Casey and Pratt (1985) and Cliff *et al.* (1989) used it to relate precaudal length (PCL, also called standard length), fork length (FL), and TL in the white shark.

Parr (1956) proposed that the ratio-on-size regressions $y/x = a + bx$ and $y/x = a + bx + bx^2$ were very convenient for graphical presentations and for practical purposes of taxonomy. Using trial-and-error fit-

ting with different ratio-on-size polynomial equations, Bass (1973) found the equation $y/x = a + bx + cx^2$ to be the most suitable for describing a large number of relative growth patterns, ranging from isometric to (simple) allometric to curvilinear, with and without minima or maxima.

Surprisingly, the allometric size-on-size equation $y = ax^b$ (power function) has rarely been used to report elasmobranch morphometry [except for reporting mass (M)-TL relationships]. However, von Bertalanffy (1960), Gould (1966), and Ricker (1979) all proposed it to be the most suitable equation for characterizing allometry.

For large sharks, such as the white shark, there has been much controversy about record sizes, especially when conversions were required from a smaller or different kind of measurement, such as PCL or M. Initially, we simply wanted to be able to convert reported M-TL equations to M-PCL equations, which requires an equation of the same form. Subsequently, we hoped to demonstrate the advantages of the allometric equation over linear size-on-size and linear ratio-on-size equations from both a theoretical and practical point of view.

Similarly, we theorized that a prolate spheroid model, obtained by rotating an ellipse around its long axis, might be useful for predicting M from length measurements (PCL) for the white shark. This

model, which assumes isometry of all dimensions, produced excellent agreement between calculated and observed M (Van Dykhuizen and Mollet, 1992) for captive sevengill sharks *Notorynchus cepedianus*. In this species, the exponent b in the M-length power equation changed from 3.33 (allometry) to 3.00 (isometry) when TL was replaced with PCL as the length variable. The white shark, which has a general body shape similar to that of the sevengill, appeared to be a suitable candidate on which to test this model.

Casey and Pratt (1985) correctly indicated that M estimates for white sharks based solely on length were questionable because of considerable variations in girth (G). They reported equations for M based on TL and G for three TL ranges. We attempt to show that a single equation, instead of three equations, could be used to predict the M of a white shark.

Materials and Methods

Data Sources

Raw morphometric data on 327 white sharks from four sources were used (Table I). We obtained data for western North Atlantic white sharks from the National Marine Fisheries Service Narragansett Laboratory. Worldwide data, including those from Australia, were obtained from two game fishing associations (J. Casey and H. L. Pratt, personal communication). Data from

the west coast of North America were obtained from three additional sources. Finally, worldwide data published by Tricas and McCosker (1984) were compared with the above data sources, and only non-overlapping data were used. Not all measurements were available from each shark; thus, the totals for some measurements are <327.

Data Analysis

We used five general equations to relate all possible combinations of morphometric measurements, each equation providing criteria for isometry and (positive) allometry (Table II). First, we used standard linear or polynomial regression to fit equations 1–4 and 5b to the data, including residual analyses (Sokal and Rohlf, 1981; Neter *et al.*, 1983). These calculations were carried out with the MGLH module of SYSTAT (Wilkinson, 1988a). This also applied to allometric equation 1, a nonlinear power function that was linearized by a logarithmic transformation: $\ln y = \ln a + b \ln y$.

Second, the geometrical mean (GM) regression was calculated for the size-on-size (and \ln size-on- \ln size) data (Ricker, 1973; McArdle, 1988). The ratio-on-size data do not require the GM regression, because the relative error of the ratio y/x is much larger than that of x (Ricker, 1973; McArdle, 1988). Thus, the ordinary (y -on- x) regression yielded the final result.

TABLE I Numbers of Morphometric Measurements for the White Shark from Various Sources

No.	Region	Measurements						Reference
		PCL	FL	TL	G	M	PCL range (m)	
1	Eastern coast of North America	59	75	71	47	61	0.96–4.47	H. L. Pratt, Jr. (personal communication), Casey and Pratt (1985), J. G. Casey (personal communication)
2	Western coast of North America			2		2		Roedel and Ripley (1950)
3	Western coast of North America		1			1		Kenyon (1959)
4	Western coast of North America			67		67	1.02–4.65	Klimley (1985a)
5	Australia		78		78	78	2.58–4.49	Casey and Pratt (1985), J. G. Casey (personal communication)
6	Worldwide			102		102	1.00–4.65	Tricas and McCosker (1984)
7	Worldwide ^a		16	3	16	16	1.17–4.31	Casey and Pratt (1985), J. G. Casey (personal communication)
Totals ^a		327	327	327	141 ^b	327	0.96–4.65	

PCL, Precaudal length; FL, fork length; TL, total length; G, girth; M, body mass.

^aMissing PCL, FL, and TL estimates calculated using geometrical mean power regression based on measurements of western North Atlantic white sharks.

^bG and M were available for 140 sharks.

TABLE II Form and Properties of Regression Equations

No.	Equation	Isometry	Positive allometry	"Good" properties	Reference
1a	$y = ax^b$	$b = 1^*$	$b > 1^*$	$y = a$ when $x = 1^t$; log transformation of 1a	Gould (1966)
1b	$\ln y = \ln a + b \ln x$				
2	$y = a + bx$	$a = 0$	$a < 0$ (negative)	$y/x = b$ when $x = \text{infinity}$	Steffens and D'Aubrey (1967)
3a	$y/x = a + bx$	$b = 0$	$b > 0$	$y/x = a$ when $x = 0$ and $y = 0$; equivalent polynomial equation ^t	Bass (1973)
3b	$y = ax + bx^2$				
4a	$y/x = a + bx + cx^2$	$b = c = 0$	$c = 0, b > 0$	General case is curvilinear; equivalent polynomial equation ^t	Parr (1956)
4b	$y = ax + bx^2 + cx^3$				
5a	$y/x = a + bx + cx/x$	$b = c = 0$	$c = 0, b > 0$	General case is curvilinear; equivalent polynomial equation ^t	Bass (1973)
5b	$y = c + ax + bx^2$				

^{*} $b = 3$ and $b > 3$ mass versus length regression.^tSuggests meters as the most convenient length unit.^tShould r^2 be used to evaluate the quality of the fit, then use equations 3b, 4b, and 5b, not 3a, 4a, and 5a.

Equation 5a was fit to the data with the help of the NONLIN module of SYSTAT (Wilkinson, 1988a) through specification of the model equation.

The GM regression parameters were calculated with the NONLIN module of SYSTAT through specification of the loss function (Fleury, 1991). They can also be obtained from the ordinary regression results, using $b(\text{GM}) = b/r$ and $a(\text{GM}) = \text{mean } y - b(\text{GM}) \text{ mean } x$. However, the NONLIN module does not produce the necessary data for a residual analysis. Therefore, residuals had to be analyzed using the results of the y -on- x regression. Similarly, the SYGRAPH module (Wilkinson, 1988b) plots the regression line with 95% confidence bands (CBs) for the y -on- x regression, but not for the GM regression. Therefore, the results of the GM regression were added to the figures. The 95% CB for the line in SYGRAPH is calculated according to the method of Neter *et al.* (1983) and is based on W statistics ($W^2 = 2F(1 - \alpha, 2, n - 2)$), rather than on t statistics. It is approximately 20–30% wider than the CB based on t statistics (Wallis and Roberts, 1956).

The quality of the fits using different fitting equations for the same data set was evaluated with the help of the t statistic of intercept and slope, standard error of estimate (SEE), residual analysis (studentized residual and leverage), and last coefficient of determination r^2 (Wilkinson, 1988a). However, the coefficient r^2 is relatively ineffective for expressing the closeness of fit and reliability of estimation of data (Whittaker and Woodwell, 1968; Bass, 1973).

The GM regression results were also used for predictions, following the recommendations and specific examples for fishery data in the work of Ricker (1973). Approximate 95% CBs for these predictions

were calculated following the method of Whittaker and Woodwell (1968).

Prolate Spheroid Approximation

Assuming isometry, maximum G at 0.5 PCL, and a weightless caudal fin, the M of a shark was approximated by assuming a prolate spheroid shape (Voellmy, 1955) and a density of 1.0 g cm^{-3} . The long axis was assumed to be the PCL of the shark. The short axis was assumed to be the diameter, $d = G/\pi$, of the shark. The available white shark data suggested that the G/PCL ratio was roughly constant (0.621 ± 0.006 SE, $N = 141$), which allowed elimination of G from the M formula and yielded $M = 20.5 (\text{kg m}^{-3})\text{PCL}^3$.

Results

Regression Results

The three two-parameter methods used to analyze the variable pairs (PCL–FL, FL–TL, PCL–TL, and G–PCL) produced equally reasonable fits (Table III). This included the ratio-on-size regressions (equation 3a), as indicated by the $r^2 = 1.0$ values of the equivalent polynomial regressions (equation 3b). Because the results were similar for all four variable pairs, we concentrated on PCL–TL. The graphical comparison of the three methods for PCL–TL indicates that the ratio-on-size regression produced the worst fit (Fig. 1). However, the ratio-on-size plot magnifies the residuals. It provided the best graphical presentation of the raw data and identified two outlying values,

TABLE III Results of Five Regression Analyses
Performed on White Shark Morphometric Measurements

No.	Equation	Description	Pair	$\ln a$	a	b	CB	N	r^2	SEE
1	$\ln y = \ln a + \ln x$	Allometric size-on-size GM power regression	ln PCL–ln FL	-0.1332	0.8753	1.0169	1.003–1.030	57	0.997	0.0213
			ln FL–ln TL	-0.1048	0.9005	1.0197	1.007–1.032	69	0.997	0.0206
			ln PCL–ln TL	-0.2427	0.7845	1.0382	1.019–1.057	58	0.995	0.0291
			ln G–ln PCL	-0.5585	0.5721	1.0798	1.038–1.121	141	0.948	0.110
			ln M–ln PCL	2.789	16.26	2.985	2.932–3.038	327	0.974	0.216
			ln M–ln TL	2.068	7.914	3.096	3.040–3.151	327	0.973	0.218
2	$y = a + bx$	Linear size-on-size GM regression; CB applies to intercept a , which determines allometry	PCL–FL	-0.038	0.9061	-0.063–(-0.013)	57	0.998	0.0424	
			FL–TL	-0.057	0.9426	-0.082–(-0.032)	69	0.988	0.0465	
			PCL–TL	-0.095	0.8550	-0.130–(-0.061)	58	0.996	0.0581	
			G–PCL	-0.169	0.6860	-0.272–(-0.066)	141	0.914	0.204	
3a	$y/x = a + bx$	Linear ratio-on-size ordinary regression	PCL/FL–FL	0.8734	0.0055	0.0008–0.010	57	0.089	0.0187	
			FL/TL–TL	0.8986	0.0066	0.0022–0.011	69	0.120	0.0186	
			PCL/TL–TL	0.7815	0.0112	0.0058–0.017	58	0.235	0.0229	
			G/PCL–PCL	0.5817	0.0140	0.0026–0.025	141	0.041	0.0686	
			M/PCL ³ –PCL	17.35	-0.336	-0.73–0.06 (NS)	327	0.009	3.699	
			M/TL ³ –TL	8.387	0.193	0.008–0.378	327	0.013	2.064	
3b	$y = ax + bx^2$	Equivalent polynomial regression of equation 3a	PCL–FL	0.8734	0.0055	0.0036–0.009	57	1.000	0.0421	
			FL–TL	0.8933	0.0083	0.0052–0.011	69	1.000	0.0439	
			PCL–TL	0.7750	0.0133	0.0093–0.017	58	0.999	0.0534	
			G–PCL	0.5654	0.0189	0.0018–0.036	141	0.989	0.203	
4a	$y/x = a + bx + cx^2$		PCL/TL–TL	0.8080	-0.010	0.0035	<i>b</i> (NS), <i>c</i> (NS)	58	0.255	0.0228
4b	$y = ax + bx^2 + cx^3$	Equivalent polynomial regression	PCL–TL	0.8265	-0.024	0.0056	<i>b</i> (NS)	58	0.999	0.0513
5a	$y/x = a + bx + cx/x$		PCL/TL–TL	0.7580	0.015	0.028	<i>b</i> (NS), <i>c</i> (NS)	58	0.239	0.0230
5b	$y = c + ax + bx^2$	Equivalent polynomial regression	PCL–TL	0.6990	0.025	0.098	<i>c</i> (NS)	58	0.997	0.0523

a, *y* intercept of regression; *b*, slope; CB, 95% confidence band; N, sample size; r^2 , coefficient of determination; SEE, standard error of estimate; GM, geometrical mean; PCL, precaudal length; FL, fork length; TL, total length; G, girth; M, body mass; NS, not significant.

which had almost identical and low PCL/TL = 0.73 without need of an analytical regression analysis. The ratio-on-size plot in Fig. 1C compared the regression lines of all three methods and indicates that they were very similar within the data range. A probability plot of the residuals and a residuals-versus-TL plot confirmed that the three methods yielded similar normal residual distributions and homoscedastic residual variances, respectively.

The GM power regression using the allometric equation gave small but significant positive allometry for PCL–FL, FL–TL, PCL–TL, and G–PCL, because the exponents, *b*, were all larger than 1.0: PCL = 0.8753 FL^{1.0169}, FL = 0.9005 TL^{1.0197}, PCL = 0.7845 TL^{1.0382}, and G = 0.5721 PCL^{1.0798}. The coefficient of determination r^2 indicated a very good fit, but the exponent, *b*, was barely significantly different from 1.0.

Likewise, the linear size-on-size GM regressions indicated positive allometry for all four length-vari-

able pairs, because the intercepts were negative (Table III). The coefficient of determination, r^2 , was close to 1.0, but the intercept (which determines allometry) was only barely significant.

The linear ratio-on-size (*y*-on-*x*) regressions produced positive slopes indicative of positive allometry for all four length-variable pairs (Table III). The coefficient r^2 was close to zero, implying a poor fit. However, the regression parameters (including the slope, which determines the amount of allometry) were statistically significant. The equivalent polynomial regressions had the highest r^2 values, and the regression lines were similar to those of the ratio-on-size regression and identical for PCL–FL (Table III). This indicated that the ratio-on-size regression itself provided good fitting equations. The SEE values of the equivalent polynomial regression were lower (i.e., better) than those of the size-on-size GM regression.

The three-parameter equations (4a and 5a) for the four length-variable pairs produced good fits, but

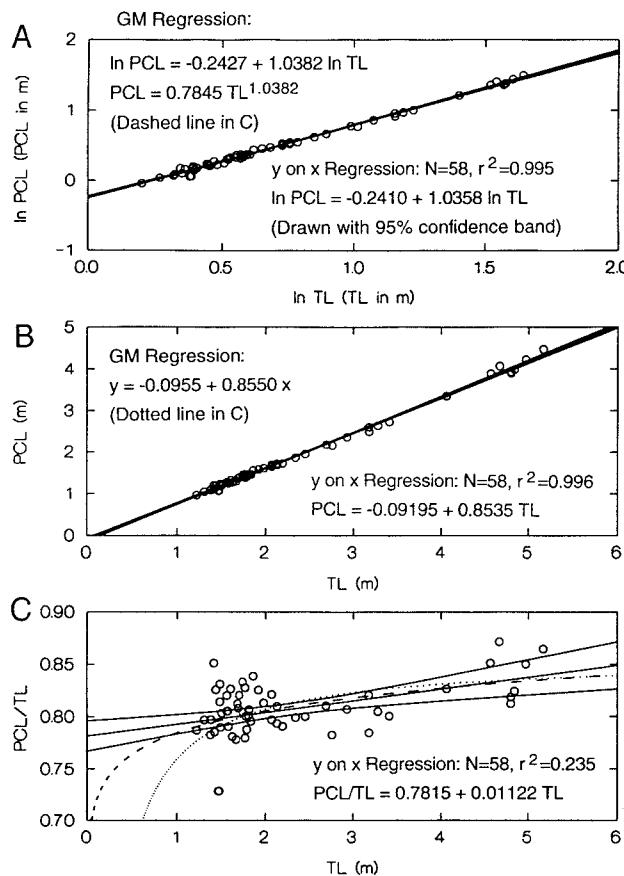


FIGURE 1 Equations for precaudal length–total length regression plots: (A) allometric (size-on-size), (B) linear size-on-size, and (C) linear ratio-on-size. The calculated geometrical mean (GM) regressions in A (dashed line) and B (dotted line) were redrawn in C for comparison. y on x regression in (B) and (C) are drawn with 95% confidence band.

they were not substantially better than any from the three two-parameter methods. The PCL/TL-versus-TL plot (Fig. 1C) indicated that a curvilinear equation with a minimum between 1.5 and 3 m TL might better fit the data. However, the regression results showed that one or more of the three parameters were not statistically significant (Table III).

The observed variation in M for sharks of similar TL or PCL was relatively large (Fig. 2 for PCL; the plots for TL are similar). A direct nonlinear fit is not shown in Fig. 2B, following the recommendation of Ricker (1979). The M -TL GM power regression indicated that b was significantly larger than 3.0 (Table III). Using this equation ($M = 7.914 TL^{3.0958}$), the median M of a 1 m TL prenatal white shark is predicted to be 7.9 kg (Table III). The M -PCL GM power regression indicated an isometric relationship because b was not significantly different from 3.0. Using this equation ($M = 16.26 PCL^{2.9851}$), the median M of a 1 m

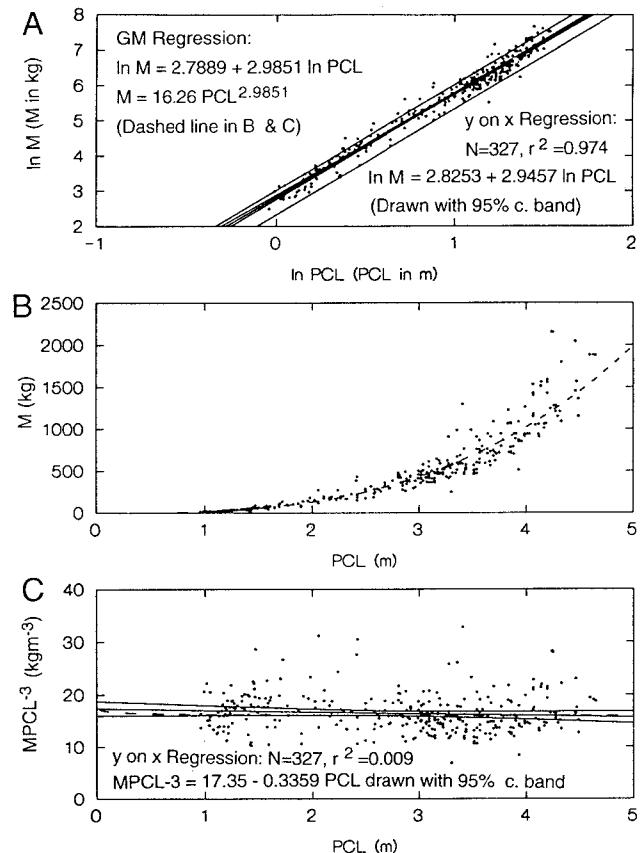


FIGURE 2 Mass (M)-precaudal length (PCL) regression plots, with 95% confidence (c.) bands. (A) Allometric equation (size-on-size; using the prolate spheroid model: top line, calculated M ; bottom line, calculated 50% of M). (B) M versus PCL data without a regression line [the calculated geometrical mean (GM) regression in A was redrawn in B (dashed line)]. (C) Linear ratio-on-size equation, with ratio M/PCL^3 [the calculated GM regression in A was redrawn in C (dashed line)].

PCL (about PCL_o) white shark would be 16.3 kg (Table III).

The ratio-on-size plots for the M -length variables provided good graphical presentation of the raw data and pointed to possible outliers (Fig. 2C for PCL). The same plot also indicated that the redrawn isometric GM regression is well within the 95% CB for the line of the ratio-on-size regression, thus verifying the latter.

The theoretical M calculations based on the prolate spheroid model provided an approximate upper limit for the observed M (upper line in Fig. 2A). Half of the calculated M agreed with an approximate lower limit for the observed M (lower line in Fig. 2A).

When Casey and Pratt's (1985) idea of using both G and TL together was applied, it provided more accurate M predictions. We used an allometric equation instead of a linear equation without a constant, and

TABLE IV Predicted Dimensions of White Sharks Using GM Power Regression

PCL (m)	FL (m) ^a	PCL/FL	TL (m) ^a	PCL/TL	G (m) ^a	G/PCL	M (kg) ^a	M/PCL ³	M/TL ³
1.000	1.140	0.877	1.263	0.792	0.572	0.572	16.3	16.27	8.07
1.100	1.252	0.879	1.385	0.794	0.634	0.576	21.6	16.25	8.14
1.200	1.364	0.880	1.506	0.797	0.697	0.580	28.0	16.23	8.21
1.300	1.476	0.881	1.627	0.799	0.759	0.584	35.6	16.21	8.27
1.400	1.587	0.882	1.747	0.801	0.823	0.588	44.4	16.19	8.33
1.500	1.698	0.883	1.867	0.803	0.886	0.591	54.6	16.17	8.39
1.600	1.810	0.884	1.987	0.805	0.950	0.594	66.2	16.15	8.44
1.700	1.921	0.885	2.106	0.807	1.015	0.597	79.3	16.14	8.49
1.800	2.032	0.886	2.226	0.809	1.079	0.600	94.0	16.12	8.53
1.900	2.143	0.887	2.344	0.810	1.144	0.602	111	16.11	8.58
2.000	2.254	0.887	2.463	0.812	1.209	0.605	129	16.10	8.62
2.100	2.365	0.888	2.582	0.813	1.275	0.607	149	16.09	8.66
2.200	2.475	0.889	2.700	0.815	1.340	0.609	171	16.07	8.70
2.300	2.586	0.889	2.818	0.816	1.406	0.611	195	16.06	8.73
2.400	2.696	0.890	2.936	0.817	1.472	0.613	222	16.05	8.77
2.500	2.807	0.891	3.054	0.819	1.539	0.615	251	16.04	8.80
2.600	2.917	0.891	3.171	0.820	1.605	0.617	282	16.03	8.83
2.700	3.027	0.892	3.289	0.821	1.672	0.619	315	16.02	8.87
2.800	3.138	0.892	3.406	0.822	1.739	0.621	352	16.01	8.90
2.900	3.248	0.893	3.523	0.823	1.806	0.623	390	16.01	8.93
3.000	3.358	0.893	3.640	0.824	1.874	0.625	432	16.00	8.95
3.100	3.468	0.894	3.757	0.825	1.941	0.626	476	15.99	8.98
3.200	3.578	0.894	3.874	0.826	2.009	0.628	524	15.98	9.01
3.300	3.688	0.895	3.990	0.827	2.077	0.629	574	15.97	9.04
3.400	3.798	0.895	4.107	0.828	2.145	0.631	628	15.97	9.06
3.500	3.908	0.896	4.223	0.829	2.213	0.632	684	15.96	9.09
3.600	4.017	0.896	4.339	0.830	2.281	0.634	744	15.95	9.11
3.700	4.127	0.897	4.455	0.831	2.350	0.635	808	15.95	9.13
3.800	4.237	0.897	4.571	0.831	2.418	0.636	875	15.94	9.16
3.900	4.346	0.897	4.687	0.832	2.487	0.638	945	15.93	9.18
4.000	4.456	0.898	4.802	0.833	2.556	0.639	1019	15.93	9.20
4.100	4.565	0.898	4.918	0.834	2.625	0.640	1097	15.92	9.22
4.200	4.675	0.898	5.034	0.834	2.694	0.642	1179	15.91	9.25
4.300	4.784	0.899	5.149	0.835	2.764	0.643	1265	15.91	9.27
4.400	4.894	0.899	5.264	0.836	2.833	0.644	1355	15.90	9.29
4.500	5.003	0.899	5.379	0.837	2.903	0.645	1449	15.90	9.31
4.600	5.112	0.900	5.495	0.837	2.972	0.646	1547	15.89	9.33
4.700	5.222	0.900	5.610	0.838	3.042	0.647	1649	15.89	9.34
4.800	5.331	0.900	5.724	0.839	3.112	0.648	1756	15.88	9.36
4.900	5.440	0.901	5.839	0.839	3.182	0.649	1868	15.88	9.38
5.000	5.549	0.901	5.954	0.840	3.253	0.651	1984	15.87	9.40
5.100	5.658	0.901	6.069	0.840	3.323	0.652	2105	15.87	9.42
5.200	5.767	0.902	6.183	0.841	3.393	0.653	2230	15.86	9.43
5.300	5.876	0.902	6.298	0.842	3.464	0.654	2361	15.86	9.45
5.400	5.985	0.902	6.412	0.842	3.534	0.655	2496	15.85	9.47

(continues)

TABLE IV (Continued)

PCL (m)	FL (m) ^a	PCL/FL	TL (m) ^a	PCL/TL	G (m) ^a	G/PCL	M (kg) ^a	M/PCL ^b	M/TL ^c
5.500	6.094	0.902	6.527	0.843	3.605	0.655	2637	15.85	9.48
5.600	6.203	0.903	6.641	0.843	3.676	0.656	2782	15.84	9.50
5.700	6.312	0.903	6.755	0.844	3.747	0.657	2933	15.84	9.52
5.800	6.421	0.903	6.869	0.844	3.818	0.658	3090	15.84	9.53
5.900	6.530	0.904	6.983	0.845	3.889	0.659	3251	15.83	9.55
6.000	6.639	0.904	7.097	0.845	3.960	0.660	3419	15.83	9.56

PCL, precaudal length; FL, fork length; TL, total length; G, girth; M, body mass.

^a95% confidence bands for predictions of FL, TL, G, and M were approximated by multiplying and dividing table entries by $e^{2\text{SEE}} = 1.06$, 1.04, 1.25, and 1.54, respectively.

this produced a better residual distribution: $\ln M = 3.65 + 0.924 \ln (G^2 TL)$, $N = 140$, SEE = 0.118, $r^2 = 0.992$. For comparison purposes, we also calculated the allometric regression of M on TL with the same N: $\ln M = 2.14 + 2.93 \ln TL$, $N = 140$, SEE = 0.178, $r^2 = 0.981$. Thus, the use of G and TL apparently produced a substantially smaller SEE. The back-transformed GM power regression using PCL was calculated for reporting purposes: $M = 45.98 (G^2 PCL)^{0.9267}$, $N = 140$, $e^{2\text{SEE}} = 1.264$, $r^2 = 0.992$.

As a result of our analysis, we can now predict one measurement from another. To provide field researchers with handy guidelines for converting or evaluating relative measurements, we have listed these calculations (Table IV). Note that there is a fairly broad CB around these predictions, especially for G and M.

Discussion

Methods

The use of the GM regression (Ricker, 1973) to calculate certain functional relationships has been criticized. Kuhr and Marcus (1977) criticized the GM regression and suggested the major axis regression to be superior. More recently, in an extensive review, McArdle (1988) compared ordinary, major axis, and reduced major axis (identical to GM) regressions and concluded that the GM regression was more efficient and less biased than the major axis regression. The GM regression was not appropriate for the ratio-on-size data, because the error of the y variable (ratio) was much larger than that of the x variable (Ricker, 1973; McArdle, 1988).

We were tempted to use the ordinary regression in order to avoid the cumbersome GM regression, be-

cause our r values were close to 1.0. However, the ordinary regression produced biased and, in some cases, unreasonable results. For example, our GM regression results indicated that the M-PCL functional relationship was isometric, whereas that for M-TL was allometric, both of which were empirically expected. The ordinary regression results indicated the reverse.

The distinction between GM and ordinary regression was not as critical for prediction purposes as it was for functional analyses. We used the GM regression for all of our functional relationships and for predictions, following Ricker's (1973) recommendations based on similar examples from the fishery literature. The ordinary regression is the proper one to use for prediction in most other cases of model II regressions (Ricker, 1973; Sokal and Rohlf, 1981; McArdle, 1988). The CB for a new observation (prediction) is much wider than that for the line (functional relationship). In our study, the GM regressions produced predictions similar to those of the ordinary regressions.

We are not convinced that a correction for back-transformation bias is necessary. Sokal and Rohlf (1981) stated that the uncorrected back-transformed response (i.e., median response) is the preferred one for biological systems with a skewed M distribution. Our corrections for bias from back-transformations, following the methods of Sprugel (1983) and Miller (1984), were negligible; the correction factor was 1.024 for M predictions from PCL, compared with a prediction CB which is approximately M/1.54 to 1.54M wide.

From the practical point of view of length conversions, all three methods tested were adequate. The available white shark data were not suitable to demonstrate the advantages of the allometric equation due to insufficient PCL, FL, and TL data for subadults

and adults, the use of nonconsistent TL measurements, and the variability or lack of accuracy of the data used. In our study of relative growth, the allometric equation produced an adequate statistical fit in most cases. It is also favored because it is simple and easily interpreted (von Bertalanffy, 1960; Gould, 1966; Ricker, 1979). We preferred the allometric equation to relate length pairs, because it allowed easy mathematical conversion between different length variables in the M-length equation.

The linear size-on-size equation is the least suitable for use with embryonic sharks (Parr, 1956). It has the mathematical property that allometry is determined by the y axis intercept, which is not reasonable from a biological point of view. Accordingly, y is not zero when x is zero, unless the relationship between y and x is isometric.

We concur with Bass (1973) and Bass *et al.* (1975) that the equation $y/x = a + bx$ successfully describes the variation of many of the proportional changes in sharks, including the white shark. Our two-parameter ratio-on-size regressions all produced normal and homoscedastic residual distributions, and we were unable to find any other possible serious drawbacks. Statistical textbooks (e.g., those by Simpson *et al.*, 1960; Sokal and Rohlf, 1981) have discussed the serious drawbacks of using ratios in statistical work. However, such ratios have proved to be most applicable in studies of the taxonomy and morphology of elasmobranchs.

Our results of large-scale morphometrics (PCL, FL, TL, and G) could be satisfactorily described with two-parameter regressions, although the need for three-parameter equations was substantiated for other white shark morphometrics (Bass *et al.*, 1975). The ratio-on-size plot is indeed excellent for a graphical presentation of the raw data and as a check for the possibility of maxima or minima. Our PCL-TL data suggested a minimum, but this could not be substantiated statistically. Two outliers with a very low PCL/TL ratio of 0.73 (Fig. 1C) were retained in the regression because they did not have high leverage. We could, however, substantiate a maximum in the first dorsal fin height versus TL ratio-on-size plot, which proved to be essential for TL validation in large white sharks (Mollet *et al.*, Chapter 10).

Regressions

Our results were in good agreement with all previously reported or updated results. Bass *et al.* (1975) reported positive simple (linear) allometry of PCL/TL versus TL: $PCL/TL = 0.803 + 0.00588 TL$ (calculated

from the given end points). The intercept was slightly higher and the allometry (slope b) was smaller, but fell within the 95% CB of our results. Casey and Pratt (1985) reported $FL = -0.068359 + 0.9517 TL$ ($N = 79$, $r^2 = 0.996$). Their results agreed well with our y -on- x results: $FL = -0.055(0.012) + 0.942(0.005) TL$, $N = 69$, $r^2 = 0.998$. Our results also agreed with the updated GM regression reported by G. Cliff and S. Dudley (personal communication): $PCL = -0.03231 + 0.9091FL$, $N = 142$, $r^2 = 0.9943$.

Cliff *et al.* (Chapter 32) also reported an updated isometric GM regression, $M = 16.504$ ($\text{kgm}^{-2.944}$) $PCL^{2.944}$ ($N = 383$, $r^2 = 0.9534$, 95% CB for $b = 2.880-3.009$), which agreed well with our $N = 327$ results: $a = 16.3$, CB of $b = 2.932-3.038$. The use of the PCL-TL exponent, $b = 1.038$, allowed conversion of reported M-TL (b range 3.15–3.20) power regression results (Compagno, 1984a; Tricas and McCosker, 1984; Casey and Pratt, 1985) to M-PCL (b range 3.03–3.08) power regression results. No CBs for b could be calculated, but we suggest that they would include $b = 3.0$, that is, isometry.

Compagno (1984a) reported $M = 8.27$ ($\text{kgm}^{-3.14}$) $TL^{3.14}$ (from 98 specimens, mostly from California, and with TLs ranging from 1.27 to 5.54 m). Assuming $r = 0.98$, $b(GM)$ was estimated to be 3.20, in agreement with our $N = 70$ California GM results: CB of $b = 3.111-3.338$. Tricas and McCosker (1984) reported $M = 7.66$ ($\text{kgm}^{-3.15}$) $TL^{3.15}$ (GM regression from 127 worldwide specimens, with TLs ranging from 1.25 to 6.4 m), and Casey and Pratt (1985) reported $M = 7.44$ ($\text{kgm}^{-3.095}$) $TL^{3.095}$ (y -on- x regression based on 200 worldwide sharks, and we estimated $b(GM) = 3.15$). These results were in agreement with our $N = 327$ GM results: $a = 7.9$ ($7.4 < 95\% < 8.5$), $b = 3.10$ ($3.04 < 95\% < 3.15$).

Prolate Spheroid Approximation

The calculated M ($M = 20.5 PCL^3$) based on the prolate spheroid approximation, using the observed mean G/PCL ratio 0.621, was 25–30% larger in the size range of 1–5 m PCL compared to the GM power regression ($M = 16.3 PCL^{2.99}$), using our data from 327 white sharks. Considering the number of approximations involved (circular vertical cross sections, elliptical longitudinal cross section with maximum G at 0.5 PCL, isometry of all dimensions, a weightless caudal fin, and a specific gravity of 1.0 gcm^{-3}), agreement to within 20–30% should be considered satisfactory. Larger calculated M was an indication that the utilized observed mean G/PCL ratio (0.621) was too large. The need of a lower effective G/PCL ratio (90%

of the observed ratio) very likely is an indication that a white shark has more taper in the back half of the body.

Mass Based on Girth and Total Length (or Precaudal Length)

Casey and Pratt (1985) indicated that M estimates for individual sharks based solely on length are questionable because of considerable G variations. Accordingly, they suggested that a more accurate M could be calculated using $M = kG^2TL$ instead of $M = aTL^b$. Initially, we thought that the use of PCL instead of TL would allow more accurate M prediction based solely on length, but the improvement was only marginal. The only improvement we can suggest is the use of the allometric equation $M = a(G^2TL)^b$ [or $M = a(G^2PCL)^b$]. These equations produced a better residual distribution, and a single equation [instead of the three equations given by Casey and Pratt (1985)] was suitable for the entire size range. The equations $M = 37.73 (G^2TL)^{0.9334}$ and $M = 45.98 (G^2PCL)^{0.9267}$ based on 140 M, G, and TL (or PCL) data points produced good (i.e., better than 20%) agreement for over 90% of the data between observed and calculated M. This was a substantial improvement over predictions based on TL (or PCL) only.

Summary

In large and relatively rare organisms such as the white shark *C. carcharias*, statistically tested conversion equations are necessary for relating different length measurements and for making M predictions. Five equations were evaluated, and we propose that the allometric equation (power function) is the most convenient for analyzing relative growth of length variables. The ratio-on-size plot is the most suitable

for a graphical presentation of raw morphometric data. The corresponding ratio-on-size regression presented no serious statistical problems. Along with M (in kilograms), data from four general sources were used: PCL, FL, TL, and G (all in meters). Parameters in the power function $y = ax^b$ were determined using a GM power regression, $\ln y = \ln a + b \ln x$, because ordinary regression produced biased results. The b 's were all significantly larger than 1.0, indicating positive allometry for PCL–FL (1.017), FL–TL (1.020), and PCL–TL (1.038). Using the PCL–TL power function, reported M–TL (b range 3.15–3.20) GM power regression results were easily converted to M–PCL (b range 3.03–3.08). Our analysis also produced M–PCL b 's close to 3.0, indicating isometry. Therefore, a constant G/PCL ratio ($x = 0.621$, $N = 141$) was used to calculate white shark M from PCL, assuming a prolate spheroid model. The results ($M = 20.5$ PCL³) were 25–30% larger (PCL range 1–5 m) than those based on the GM power regression ($M = 16.3$ PCL^{2.99}, $N = 327$). More accurate M prediction ($\leq 20\%$ for individual sharks) required the use of G and PCL according to $M = 46.0 (G^2PCL)^{0.927}$ ($N = 140$).

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GREAT WHITE SHARKS

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