

THE RELATIONSHIP BETWEEN HEART MASS AND
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NARROW ALLOMETRY DEMONSTRATES
INTERSPECIFIC DIFFERENCES

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THE RELATIONSHIP BETWEEN HEART MASS AND BODY MASS FOR THREE CETACEAN GENERA: NARROW ALLOMETRY DEMONSTRATES INTERSPECIFIC DIFFERENCES

It has become common practice in comparative animal studies to examine allometric relationships between body mass and a second morphological or physiological measure (see Calder 1984 and Schmidt-Neilsen 1984 for reviews). These relationships often permit generalizations about relative changes in one organ or physiological process with respect to another over a wide range of body sizes. The utility of such relationships is readily apparent particularly when applied to wild populations in which extensive physiological measurements are not possible. For example, basal metabolic rate of the blue whale (Lavigne *et al.* 1990) has been estimated using Kleiber's (1975) equation. Mathematically, body-size relationships are often of the form of a power relation: the variable expected to depend on body size is expressed as a function of body size raised to some power. Statistical analyses of such body-size relationships are simplified by log transforming the data and analyzing the relationships as straight lines. While broad scale allometric relationships are appealing, both for their apparent applicability over a wide range of body sizes and their mathematical simplicity, their use may mask important interspecific differences which are evident only when analyzing over a narrow range of body size.

Brody (1945) fitted an allometric equation to heart mass (kg) as a function of body mass (kg) for adult mammals ranging in body size from 0.01 to over 100,000 kg. Innes *et al.* (1986) observed that the mass exponent in Brody's equation, $H = 0.00588M^{0.984}$ where H is heart mass and M is body mass, is not different from 0.94 derived for cetacean species (Sergeant's data 1969). Lockyer (1981) also showed that Brody's equation seems to fit heart mass data for cetaceans as different as *Phocoena phocoena* and *Balaenoptera musculus*. Ridgway and Johnston (1966), however, reported differences in heart mass as a percent of body mass between the three species *Phocoenoides dalli*, *Lagenorhynchus obliquidens* and *Tursiops truncatus*. Heart mass estimates made from a general allometric equation such as Brody's or Innes's will fail to demonstrate differences in heart masses, if they do exist, between species whose body sizes overlap. Limiting the range of body sizes over which these equations are fit may provide insight into physiological, morphological, or behavioral variation between species

(Smith 1984). We present heart mass and body mass values from three genera of small odontocetes in which interspecific differences in scaling do exist, and propose an explanation based on ecological and physiological differences.

We compared relative heart masses of four species of small odontocetes in the 50–234 kg body mass range, a range over 500 times smaller than the one used by Brody (1945). Data on *Lagenorhynchus acutus* are from the study of Geraci *et al.* (1978); and on *Phocoenoides dalli* from Morejohn (1979), the study of Ridgway and Johnston (1966) and N. Miyazaki (personal communication). In addition, we have included previously unpublished data from our laboratory on *L. obliquidens*, *P. dalli*, and *T. truncatus*. Since not all the studies provided information about the sexual maturity of the individuals, we divided the data set into two groups based on body mass. *T. truncatus*, *P. dalli*, and *Lagenorhynchus* spp. were considered adult if their body masses exceeded 120, 75, and 75 kg, respectively, while smaller individuals were considered juveniles (S. Ridgway, personal observation). All data are from either strandings, incidental takes by fisheries, or from animals which died of natural causes while being maintained in our program under U.S. Federal permit. We agree with Calder (1984) who emphasized the value of publishing complete data sets for allometric studies; therefore, we have listed all of our data in Table 1.

A least-squares analysis was carried out on both the untransformed data and log transformed data in order to determine the relationships between heart mass and body mass. While the untransformed data over such a small body size range appeared linear, the slopes of the best-fit lines for the log transformed data were found to be significantly different from 1 (juveniles: $P = 0.037$, adults: $P < 0.001$) using Student's *t*-tests followed by a consensus combined *P*-value test (Rice 1990). The log transformation also resulted in a decrease in heteroscedasticity within each data set. Therefore, an allometric relationship for each of the four species (three genera) and two size classes was described by a linear equation of the form $\log M_h = \log a + b \log M_b$, where M_h is heart mass (kg) and M_b is body mass (kg).

For the adult individuals, slopes of the resultant regression lines were compared using an *F*-test (Wall 1986) and found not to differ ($P = 0.158$). Since the slopes were not significantly different, the regression lines were recalculated using a common slope. Intercepts of the parallel lines were compared using an *F*-test and found to differ ($P < 0.001$). Student's *t*-tests comparing each pair of intercepts followed by a sequential Bonferroni adjustment for multiple comparisons (Rice 1989) showed no difference between the lines of *L. acutus* and *L. obliquidens* ($P = 0.107$). All other pairs of lines had different intercepts ($P < 0.001$). The results of the analysis with four species allowed us to pool the *Lagenorhynchus* spp. data and repeat the regression analyses for the three genera. Slopes again were found not to differ ($P = 0.158$). A common slope was determined and intercepts of the parallel lines were compared and found to differ ($P < 0.001$). Student's *t*-tests comparing each pair of intercepts followed by a sequential Bonferroni adjustment for multiple comparisons demonstrated significant differences in intercepts of each of the three lines ($P < 0.001$).

Identical analyses were run with the juvenile data. Slopes of the resultant

Table 1. Body mass (M_b) and heart mass (M_h) for the four dolphin species in kg. Data followed by "*" are from Morejohn (1979); data followed by "#", are from N. Miyazaki (personal communication); data followed by "&" were provided by Geraci *et al.* (1978); unmarked data are from our laboratory.

M_b	<i>Phocoenoides dalli</i>						<i>Lagenorhynchus acutus</i>						<i>L. obliquidens</i>						<i>Tursiops truncatus</i>					
	Adults		Juveniles		Adults		Juveniles		Adults		Juveniles		Adults		Juveniles		Adults		Juveniles		Adults		Juveniles	
	M_b	M_h	M_b	M_h	M_b	M_h	M_b	M_h	M_b	M_h	M_b	M_h	M_b	M_h	M_b	M_h	M_b	M_h	M_b	M_h	M_b	M_h	M_b	M_h
82	0.876*	73	0.739*	152	1.120&	58	0.475&	100	0.660	72	0.470	130	0.544	97	0.607									
95	0.913*	73	0.640*	234	1.400&	56	0.400&	90	0.655	58	0.385	125	0.650	119	0.835									
97	0.864*	65	0.700#	182	1.180&	69	0.550&	85	0.640	59	0.400	182	0.781	86	0.413									
213	1.680*	54	0.510#	188	1.100&	69	0.570&	80	0.701	57	0.542	126	0.575	98	0.607									
149	1.232*	66	0.670#	163	1.060&	69	0.580&	76	0.545	73	0.655	172	0.769	90	0.449									
82	0.708*	68	0.520#	152	1.080&	66	0.600&	74	0.820	197	0.688	145	0.680	68	0.320									
88	0.881*	50	0.460#	150	1.100&	61	0.490&	127	0.555	149	0.600	131	0.538	95	0.350									
81	0.672*	65	0.610#	164	1.220&	170	1.080&	186	0.885	152	0.763	130	0.462	64	0.530									
89	0.950#	54	0.470#	160	1.080&	158	1.225&	151	1.060&	144	1.075&	174	0.895	50	0.250									
96	0.900#	68	0.615#	152	1.120&	151	1.050&	148	1.010&	155	1.150&	158	0.750	184	1.099									
100	1.000#	58	0.550#	138	1.000&	207	1.230&	155	1.130&	136	1.050&	170	0.771	86	0.413									
101	0.980#	71	0.560#	207	1.230&	144	1.075&	135	0.875&	159	1.250&	184	1.099	86	0.413									
86	0.880#	71	0.600#	170	1.080&	158	1.225&	155	1.150&	148	1.010&	155	1.130&	136	1.050&									
124	1.110#	61	0.560#	158	1.225&	151	1.060&	144	1.075&	135	0.875&	159	1.250&	136	1.050&									
107	1.000#	62	0.720#	151	1.060&	144	1.075&	135	0.875&	159	1.250&	136	1.050&	136	1.050&									
89	0.874#	73	0.790#	144	1.075&	135	0.875&	159	1.250&	136	1.050&	136	1.050&	136	1.050&									
105	0.839#	71	0.690#	135	0.875&	159	1.250&	136	1.050&	136	1.050&	136	1.050&	136	1.050&									
126	1.220#	63	0.580#	159	1.250&	136	1.050&	136	1.050&	136	1.050&	136	1.050&	136	1.050&									
82	0.770#	70	0.753#	155	1.150&	148	1.010&	155	1.130&	136	1.050&	136	1.050&	136	1.050&									
78	0.810#	62	0.555#	148	1.010&	155	1.130&	136	1.050&	136	1.050&	136	1.050&	136	1.050&									
76	0.785#	64	0.587#	155	1.130&	136	1.050&	136	1.050&	136	1.050&	136	1.050&	136	1.050&									
149	1.200#	70	0.690#	136	1.050&	136	1.050&	136	1.050&	136	1.050&	136	1.050&	136	1.050&									
154	1.390#	63	0.550#	175	1.240&	136	1.050&	136	1.050&	136	1.050&	136	1.050&	136	1.050&									

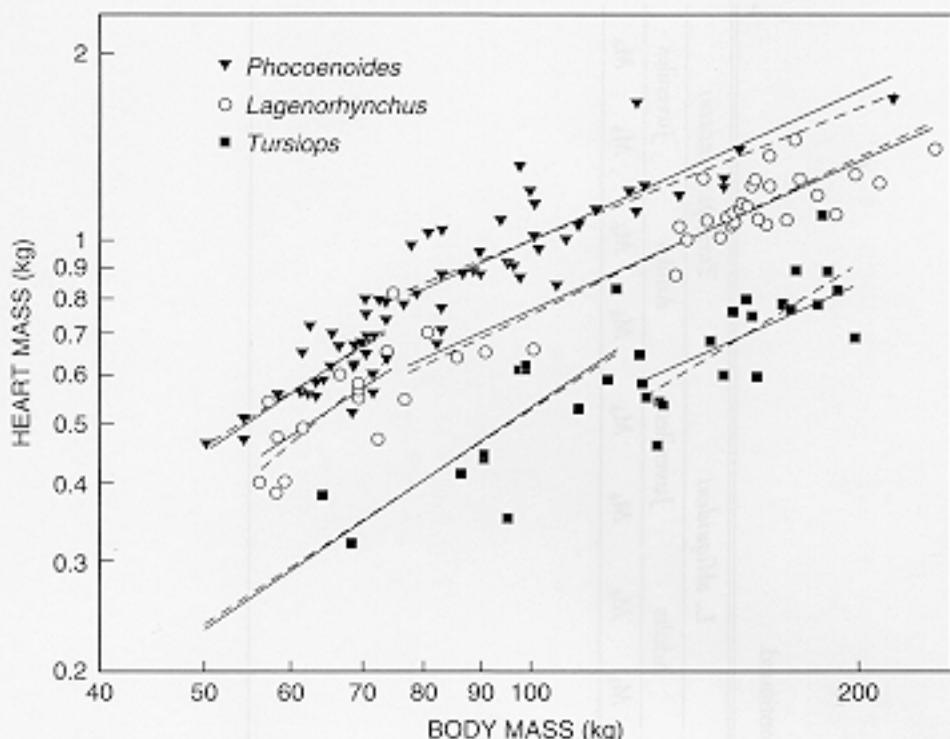


Figure 1. Heart mass to body mass relationships for the three dolphin genera. Data sources are given in Table 1. The dashed lines are least-squares estimates of the log transformed data. Solid lines are those fit under the constraint of a constant slope. Discontinuities in the lines for each genus occur at the transition between the two size classes.

regression lines were compared and found not to differ ($P = 0.772$). A common slope was calculated and intercepts of the parallel lines were compared and found to differ ($P < 0.001$). A comparison between each pair of intercepts demonstrated no difference between the lines of *L. acutus* and *L. obliquidens* ($P = 0.877$). All other pairs of lines had different intercepts ($P < 0.02$). The *Lagenorhynchus* spp. data were pooled and the regression analyses repeated for the three genera. Slopes again were found not to differ ($P = 0.582$). A common slope was determined and intercepts of each parallel line were compared and found to differ ($P < 0.001$). Thus, for both juveniles and adults, we demonstrated a difference in relative M_h between the three genera: *Phocoenoides* had the largest hearts in relation to body size, *Tursiops* the smallest, and the *Lagenorhynchus* spp. a relative heart mass intermediate of the three genera studied (Fig. 1). Coefficients and standard errors for each of the resultant allometric equations relating heart mass and body mass are given in Table 2.

To determine whether the size, and thus inferred maturation state, is a significant determinant of heart mass, we compared, *via* a general linear model *F*-test (Neter *et al.* 1985), a single linear regression for all the data within a genus with regressions for the same data divided into the two size classes.

Table 2. Coefficients and standard errors of the allometric relationships, $\log M_h = \log a + b \log M_b$, relating heart mass and body mass. Numbers in parentheses are sample sizes.

Genera	$\log a$	$SE_{\log a}$	b	SE_b	$S_{y,x}$	r^2
<i>Phocoenoides</i>						
Adults (35)	-1.614	0.116	0.808	0.057	0.059	0.595
Juveniles (30)	-2.373	0.215	1.195	0.118	0.045	0.523
<i>Lagenorhynchus</i>						
Adults (28)	-1.729	0.125	0.808	0.057	0.042	0.839
Juveniles (13)	-2.443	0.214	1.195	0.118	0.067	0.489
<i>Tursiops</i>						
Adults (20)	-1.927	0.127	0.808	0.057	0.062	0.544
Juveniles (15)	-2.660	0.229	1.195	0.118	0.072	0.734

$SE_{\log a}$ = standard error of $\log a$.

SE_b = standard error of the common mass exponent b .

$S_{y,x}$ = standard error of the estimated line.

r^2 = coefficient of determination.

Individual tests for each genus were pooled using a consensus combined P -value test (Rice 1990), and the size effect was found to be significant ($P < 0.001$). Thus, where Brody (1945) indicates that heart mass tends to vary directly with body mass during growth, we demonstrate that heart mass is significantly greater in proportion to body mass in small growing animals. Perrin and Roberts (1972) report similar findings for *Stenella attenuata*.

Since our narrow scale allometric analysis demonstrates significant differences in the scaling of heart mass with body mass in these three cetacean genera, we suggest that these observed differences may be due to differences in physiological and ecological demands. From studies on terrestrial species it is known that individuals with greater metabolic demands due to exercise or high thermoregulatory costs have greater heart masses (Astrand and Rodahl 1977). *P. dalli* is primarily an offshore, cool-water porpoise (Gaskin 1982) yet has thin blubber, comparatively large muscle mass, and is reported to be one of the fastest swimming of small cetaceans (Norris and Prescott 1961, Ridgway 1966). *L. acutus* and *L. obliquidens* have antitropical distributions in the North Atlantic and North Pacific respectively (Gaskin 1982) and are reported to be slower swimmers than *P. dalli* (Norris and Prescott 1961, Ridgway and Johnston 1966). All of the *Tursiops* measurements reported here were of Atlantic bottlenose dolphins from the Gulf of Mexico. These *Tursiops* are known to be a slower moving species preferring warmer, nearshore waters yet have thicker blubber in comparison to *Phocoenoides* and *Lagenorhynchus*. *P. dalli* feeds primarily on squid near the thermocline of deeper waters (Gaskin 1982) and on some deep-water fish species such as hake (Norris and Prescott 1961). Stomach content analysis of a group of stranded *L. acutus* (Geraci *et al.* 1978) also demonstrates a diet of both squid and fish, however they are generally fish eaters and may spend less time diving to the deep thermocline (Gaskin 1982). Al-

ternatively, *T. truncatus* populations from the Gulf of Mexico rarely feed offshore and have diets consisting primarily of nearshore fishes (Barros and Odell 1990). *P. dalli*, *L. obliquidens*, and *T. truncatus* individuals of approximately the same body mass required 14.5, 8.5, and 6.0 kg, respectively, of Pacific mackerel per day to maintain body weight (Ridgway and Johnston 1966), again supporting parallel differences in metabolic rates.

In addition to behavioral and distributional differences, Ridgway and Johnston (1966) found marked differences in the blood volumes of *P. dalli*, *L. obliquidens*, and *T. truncatus* (143, 108, and 71 ml/kg, respectively). Similarly they report differences in mean packed-cell volumes for the three species at 57, 53, and 45 percent, respectively, contributing to overall differences in blood-oxygen carrying capacities of the three species. Increased dive capabilities associated with the higher oxygen carrying capacities (Kooyman 1985) are substantiated by observations in these three genera.

It is interesting to note that when we examined relative heart masses of two *Stenella* species of the eastern tropical Pacific reported by Perrin and Roberts (1972), we found heart masses still lower than those of the three genera reported here.

Regarding the present analysis, we conclude that broad scale allometric relationships may not be appropriate for comparisons between species of a similar size. A slope coefficient generated from pooled data may deviate from the true slopes for the individual species' data whenever the relationships for the individual species do not have both the same slopes and intercepts (Heusner 1982). We pooled the heart mass data for the adults of the three genera reported here with the *Stenella* spp. adults from Perrin and Roberts' study (1972) and derived the relationship $\log M_h = -2.252 + 1.037 \log M_b$, where M_h is heart mass (kg) and M_b is body mass (kg). Thus, by pooling data for four genera shown to have different relative heart masses, we have derived an isometric relationship (slope not different from 1, $P = 0.672$) consistent with previous interspecific relationships. The common slope of 0.808 reported here when each genus is permitted to have a unique intercept, is significantly different from 1 ($P = 0.001$).

In agreement with Smith (1984) we have found that the application of "broad allometry" techniques, although widely used in comparative studies, may be insufficient for comparisons between genera within a small body size range. Different species, or even populations of animals of the same species and body size, will not necessarily share the same ecological niche or physiological characteristics. In our view it is a worthwhile biological question to ask why *P. dalli* has a heart significantly larger than that of *T. truncatus*, a distinction which might be overlooked when relationships over large body size ranges are examined.

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