

Abstract.—Interest in estimating energy fluxes through populations of marine mammals has been increasing as these populations are more frequently recognized to compete with fishermen for commercially exploited fish stocks. Testing for the presence of allometric trends with size in the parameters used to estimate these energy fluxes is important because if such trends exist and are large, it will be inappropriate to apply measurements derived from one size of animal to animals of other sizes, in any given population. To test for (and to measure, if present) allometric effects in a population of small cetaceans, morphological measurements (energetics parameters) related to estimating energy flux were taken from 35 spotted dolphins (*Stenella attenuata*) ranging in size from 77 to 210 cm total length, captured incidental to fishing operations in the eastern tropical Pacific Ocean.

Significant allometric (nonlinear) changes with size were observed in 23 of the 25 parameters measured; no trends were isometric (linear). Most of the significant trends were expressed primarily during the first two or three years of life (5–30 kg wet weight). Thus, parameter estimates for small dolphins (less than about 30 kg wet weight) should be derived from measurements on animals near the specific size of interest. Estimates for larger animals, with the exception of several surface area measurements, could be estimated reasonably well from any specimens greater than about 30 kg wet.

Although the energy fluxes and standing stock of energy represented by animals younger than 2–3 years are relatively small compared with the total population, constraints resulting from the energy characteristics of the smaller animals may exert significant control over population energy flux, implying that the rapid changes in energetics parameters of the younger animals should not be ignored.

Allometry of energetics parameters in spotted Dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean

Elizabeth F. Edwards

Southwest Fisheries Science Center
P.O. Box 271, La Jolla, CA 92038

Estimating cetacean population energy fluxes, in particular energy consumption in the form of commercially valuable fishes, is important because many commercially exploited fish populations are decreasing in abundance yet must be shared by both human and cetacean predators. The existence in cetacean populations of allometric trends (nonlinear changes with size) in morphological characteristics related to energy processing complicates energy flux estimation for these animals because the size range of cetacean specimens available for study tends to be very narrow. If allometric trends are present and large, measurements from that narrow size range cannot be assumed to apply equally to all other sizes in the population.

Neither commercial nor noncommercial sources of cetacean specimens generally provide an adequate range of sizes from which to determine whether allometric trends exist. Specimens available from commercial sources will include only those sizes sought by the fishery. For example, morphological samples from large cetaceans (whales) tend to be dominated by adult (and when pregnant females are captured, by fetal) specimens because the larger individuals have more commercial value. Juveniles are rarely captured. Morphological samples from small cetaceans (dolphins and porpoises) are rare for all sizes because these animals are rarely the subject of directed

fisheries. Specimens from noncommercial sources are generally available only as beached or stranded individuals, or where observer programs are employed to monitor kill rates of both target and nontarget species. These noncommercial specimens tend to be too rare to provide an adequate sample of sizes.

In addition to these sampling biases in age and species composition, the data collected are generally unsuitable for deriving estimates of energy flux. Although considerable morphological data exist for commercially exploited large whales (e.g., Fujino 1954, 1956; Omura and Fujino, 1954; Omura and Sakiura, 1956; Ohsumi, 1960; Nishiwaki et al., 1963; Lockyer, 1981, a and b, and references therein) and a few similar reports exist for small cetaceans (e.g., Sergeant, 1962; Perrin, 1975; Yasui, 1980; Perrin et al., 1987), these data generally include only a standardized set of external morphological measurements used primarily for taxonomic purposes. Taxonomic data tend to be inappropriate for deriving estimates of energy flux because many size classes and most of the morphological measurements required specifically for energetics estimates are missing.

Although some estimates have been developed for energy processing in neonate through adult large whales (Lockyer, 1981, a and b), allometric trends in energetics parameters have never been examined in

small cetaceans. Existing studies of small cetaceans include only Yasui and Gaskin's (1986) energy budget for adult harbor porpoise (*Phocoena*), in addition to a few estimates for various aspects of energy processing by juvenile (e.g., Anderson, 1981) or adult (e.g., Lang, 1966; Lockyer, 1981, a and b; Yasui and Gaskin, 1986; Hui, 1987; Bose and Lien, 1989; Bose et al., 1990) small cetaceans.

Incidental mortality of spotted dolphins (*Stenella attenuata*), a small cetacean that is inadvertently killed during some tuna purse-seining operations in the eastern tropical Pacific Ocean (ETP), presents an exception to this problem of specimen unavailability. Specimens of all sizes die in purse-seines (Barlow and Hohn, 1984; Hohn and Hammond, 1985), making it possible to collect appropriate data for the entire size range occurring in the natural population.

Taking advantage of this availability of specimens, spotted dolphins ranging in size from fetal through mature adult were collected from the fishery and analyzed for morphological characteristics related to energy processing. I report here regression equations relating changes in 25 energetics parameters to changes in total wet weight for these specimens. The parameters can be used in estimation of three components contributing to cetacean energy budgets: active metabolism, passive heat loss, and energy density. Estimated energy density is derived from a subset of the measured parameters and is reported as the 25th parameter. Total energy budgets, active metabolism, and passive heat loss are not estimated here because such estimates depend on various assumptions about other factors (e.g., environmental conditions, activity levels) and other energy budget components (e.g., standard metabolism, heat of digestion) not included in this study. The work reported here was conducted to determine the extent to which allometric trends, if any, could be determined from simple morphological measurements on deceased cetaceans.

Methods and materials

Specimen collection

Measurements were taken from 35 spotted dolphins ranging in size from 71 to 210 cm total length (TL [tip of rostrum to fluke notch] Fig. 1). This represents the entire size range (near-term fetus through mature adult) of the spotted dolphins found in

the eastern tropical Pacific Ocean (spotted dolphins are about 80 cm total length at birth (Hohn and Hammond, 1985)). Specimens included 22 females and 13 males (Table 1). Males specimens included 3 fetuses, 6 immature, and 4 mature. Females specimens included 3 fetuses, 6 immature, 1 mature resting, 1 mature lactating, and 11 mature pregnant. Not all measurements were made on all specimens. All specimens were collected incidental to tuna fishing operations in the eastern tropical Pacific Ocean. Seventeen of the specimens were collected on 28 December 1985; nine were collected during July and two during August 1985 (Table 1). Specimens were kept frozen after collection and were thawed in fresh water (about 27°C) just prior to sampling for energetics parameters.

Parameter measurements

Active metabolism Active metabolism in cetaceans is the total energy cost of swimming, i.e., energy (mechanical plus waste heat production heat) expended to overcome hydrodynamic drag. Cost of steady submerged swimming by cetaceans can be estimated by using Magnuson's (1978) procedure for estimating cost of swimming by tuna (see also Webb, 1975), including drag on both body and fins. Eleven morphological measurements are required to estimate hydrodynamic drag: maximum diameter of the body (D_{max}); wetted surface areas of the body (WSA_b), flippers (WSA_{fp}), dorsal fin (WSA_d), and flukes (WSA_f); mid-chord depths of flippers (MCD_{fp}), dorsal fin (MCD_d), and flukes (MCD_f); and characteristic length of flippers (CL_{fp}), dorsal fin (CL_d), and flukes (CL_f) (Table 2).

D_{max} was derived from measurements of body circumference immediately anterior to the dorsal fin (C_3 ;

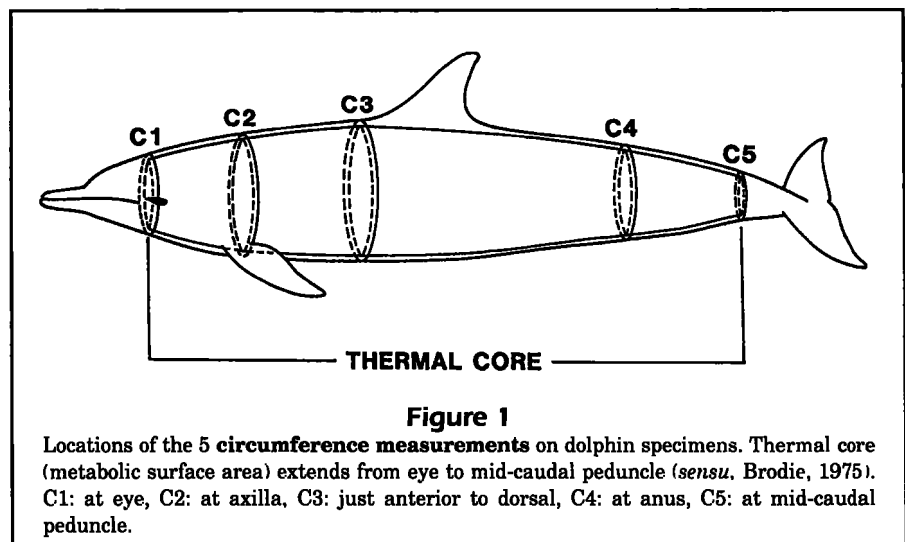


Figure 1

Locations of the 5 circumference measurements on dolphin specimens. Thermal core (metabolic surface area) extends from eye to mid-caudal peduncle (*sensu*, Brodie, 1975). C1: at eye, C2: at axilla, C3: just anterior to dorsal, C4: at anus, C5: at mid-caudal peduncle.

Table 1
Collection data for dolphin specimens.

Specimen no.	Spec. Code	wet weight (gm)	total length (cm)	Sex	Reprod. ¹ condition	Date captured	Location (lat.)	Captured (long.)	D_{max} (cm)	BD_o (cm)
1	BXR252	27013	132	F	I	12/28/85	17°46'N	111°37'W	71.8	0.75
2	BXR253	68100	194	F	M-R	12/28/85	17°46'N	111°37'W	95.0	0.97
3	BXR254	73775	192	F	M-P	12/28/85	17°46'N	111°37'W	103.2	0.86
4	BXR254F	4983	78	M	F	12/28/85	17°46'N	111°37'W	35.4	0.45
5	BXR255	64540	186	F	M-P	12/28/85	17°46'N	111°37'W	107.5	1.08
6	BXR255F	5800	78	F	F	12/28/85	17°46'N	111°37'W	40.8	0.68
7	BXR264	62425	183	F	M-P	12/28/85	18°09'W	111°17'W	97.8	0.82
8	BXR264F	3760	71	F	F	12/28/85	18°09'W	111°17'W	34.0	0.51
9	BXR271	24516	136	M	I	12/28/85	18°09'W	111°17'W	66.9	0.83
10	BXR280	19976	127	M	I	12/28/85	18°09'W	111°17'W	61.0	0.68
11	BXR282	76272	193	F	M-P	12/28/85	18°09'W	111°17'W	103.0	1.00
12	BXR295F	4200	74	F	F	12/28/85	18°09'W	111°17'W	34.6	0.52
13	BXR306	37228	163	F	I	12/28/85	18°09'W	111°17'W	75.0	0.90
14	BXR312	35639	152	F	I	12/28/85	18°09'W	111°17'W	75.0	0.88
15	BXR313	63787	175	F	M-P	12/28/85	18°09'W	111°17'W	97.6	0.92
16	BXR(A)284F	3410	71	M	F	12/28/85	18°09'W	111°17'W	34.8	0.45
17	BXR(A)284	69689	191	F	M-P	12/28/85	18°09'W	111°17'W	100.4	NR
18	SRMO44(F)	5400	81	M	F	2/14/80	06°02'S	85°46'W	40.0	0.73
19	WFP660	16400	114	F	I	NR	NR	NR	55.0	NR
20	WFP680	30900	136	M	I	7/7/83	NR	NR	74.0	NR
21	SRMO44	73100	189	F	M-P	2/14/80	06°02'S	85°46'W	110.0	0.97
22	WFP700	48124	170	M	M	NR	NR	NR	84.6	0.61
23	PEL307	42903	167	F	I	7/10/85	8°55'N	129°58'W	80.0	0.70
24	PEL308	41314	151	M	I	7/10/85	8°55'N	129°58'W	81.0	0.72
25	PEL309	74002	189	F	M-P	7/13/85	8°13'N	129°40'W	99.0	0.95
26	PEL310	71732	202	F	M-P	7/13/85	8°13'N	129°40'W	97.5	0.85
27	PEL311	55388	176	F	M-P	7/14/85	10°21'N	129°35'W	91.0	NR
28	PEL313	72640	202	M	M	7/14/85	10°21'N	129°35'W	94.2	0.66
29	PEL314	44265	160	M	I	7/14/85	10°21'N	129°35'W	85.4	0.69
30	PEL315	69008	188	M	M	7/14/85	10°21'N	129°35'W	95.5	0.82
31	PEL316	58566	175	F	M-P	7/14/85	10°21'N	129°35'W	94.0	0.87
32	SD1	11350	100	M	I	NR	NR	NR	53.5	0.71
33	SD2	14301	113	F	I	NR	NR	NR	56.0	0.61
34	STB122	84444	206	M	M	8/30/85	10°14'N	125°03'W	98.0	0.86
35	STB126	74202	188	F	M-L	8/30/85	10°14'N	125°03'W	102.0	0.64

¹F = fetus; I = immature; M = mature; M-R = mature resting; M-P = mature pregnant; M-L = mature lactating; NR = no record.

Fig. 1). WSA_p was measured as the sum of surface areas of right circular cones. Conic surfaces were calculated from measurements of body circumference at five locations and distances from tip of rostrum to each circumference and to fluke notch (Fig. 1).

WSA_p , WSA_d and WSA_f were estimated by tracing the perimeter of each fin onto white paper, measuring with a digitizer the surface enclosed, correcting for curvature, and multiplying by 2. Both flukes were traced as a unit. Each dorsal fin and flipper were traced separately.

The correction for curvature along fin surfaces was derived from one small (132 cm TL) and one large (193 cm TL) dolphin. Flippers, flukes, and dorsal fin

from each specimen were sliced laterally into 4 or 5 sections. The cross-section of each piece was then xeroxed onto white paper. Distances straight across and around the perimeter of each cross-section were then measured twice for each cross-sectioned piece of fin. There were no significant differences between fins or sizes of dolphin in the ratio of curved to flat measurements so a single correction was used for all fins. The curvature correction was an increase of 6% over the estimated flat area of each fin (3% per side; SE = 0.4; $n = 23$ sections).

MCD_p , MCD_d , and MCD_f were measured to the nearest millimeter by using calipers at the thickest part of each fin at the mid-point of the characteristic length.

Table 2
Symbols and definitions.

<i>ACT</i>	active metabolism (calories active metabolism/calorie animal ⁻¹ ·hr ⁻¹)
<i>BD_a</i>	average blubber depth (cm)
<i>C_f</i>	coefficient of friction drag
<i>C_T</i>	coefficient of total drag
<i>CD_d</i>	caloric density of dolphin (cal/g wet weight ⁻¹)
<i>CL_{fp}</i>	characteristic length of the flippers (cm)
<i>CL_b</i>	characteristic length of the dorsal fin (cm)
<i>CL_f</i>	characteristic length of the flukes (cm)
<i>D_{max}</i>	maximum diameter of the body (cm)
<i>D_T</i>	total drag (dyn)
<i>ED_{an}</i>	energy density of total animal (mJ/kg wet weight)
<i>ED_{bl}</i>	energy density of blubber (mJ/kg wet weight)
<i>ED_m</i>	energy density of muscle (mJ/kg wet weight)
<i>ED_b</i>	energy density of bone (mJ/kg wet weight)
<i>F_m</i>	fraction of body wet mass due to muscle
<i>F_{bl}</i>	fraction of body wet mass due to blubber
<i>F_b</i>	fraction of body wet mass due to bone
<i>F_v</i>	fraction of body wet mass due to viscera
<i>F_f</i>	fraction of body wet mass due to fins
<i>FID</i>	fin-induced drag (fraction of total drag)
<i>H_u</i>	minimum unavoidable heat loss (calories lost as heat/calorie animal ⁻¹ ·day ⁻¹)
<i>MCD_{fp}</i>	mid-chord depth of the flippers (cm)
<i>MCD_b</i>	mid-chord depth of the dorsal fin (cm)
<i>MCD_f</i>	mid-chord depth of the flukes (cm)
<i>ME</i>	mechanical efficiency
<i>MP</i>	mechanical power (erg/s)
<i>MSA_b</i>	metabolic surface area of the body (cm ²)
<i>N</i>	density of sea water (g/cm ³)
<i>PE</i>	propeller efficiency
<i>R_L</i>	Reynolds number based on length <i>L</i> (dyn/cm ²)
<i>TL</i>	total length (cm)
<i>ν</i>	kinematic viscosity (stoke)
<i>VL</i>	velocity (cm·sec ⁻¹)
<i>WSA_b</i>	wetted surface area of the body (cm ²)
<i>WSA_{fp}</i>	wetted surface area of the flippers (cm ²)
<i>WSA_d</i>	wetted surface area of the dorsal fin (cm ²)
<i>WSA_f</i>	wetted surface area of the flukes (cm ²)
<i>WW_g</i>	total body wet weight (g)
<i>%H₂O_{bl}</i>	water content of blubber (percent of wet weight)
<i>%H₂O_m</i>	water contents of muscle (percent of wet weight)
<i>%H₂O_b</i>	water contents of bone (percent of wet weight)

CL_{fp}, *CL_d*, and *CL_f* were estimated from the traced figures, by measuring the length of the fin parallel to the main axis of the body.

Unavoidable passive heat loss (*HL_u*) Unavoidable passive heat loss was defined as heat loss due to conduction through blubber, if one assumes no heat loss from appendages or from the head anterior to the eyes (e.g., Brodie, 1975). Two morphological measurements contribute to this estimate of *HL_u*; metabolic surface area of the body (*MSA_b*) and average blubber depth (*BD_a*). *MSA_b* was estimated by the same method as wetted surface area, except that the first anterior and

last posterior sections of the body (Fig. 1) were omitted from the assumed thermal core and the conic radius used in the estimate was the radius of the body core beneath the blubber. This metabolic radius was estimated by determining the radius to the outer surface at each circumference and by subtracting the average blubber depth measured at that circumference. Two or three measurements of blubber depth were made along each circumference at the dorsal midline, ventral midline, and mid-way between these two lines.

BD_a for the entire animal was estimated as the weighted sum of average blubber depths at each circumference. Weightings were the circumferences themselves, which gives more weight to the relatively symmetrical mid-body areas that comprise the majority of the insulating area, and less weight to the thick average blubber depths related to the hydrodynamic keel in the tail region.

Energy density Eleven morphological measurements contribute to estimating the overall energy density of an individual spotted dolphin (*ED_{an}*): fractions of wet mass due to muscle (*F_m*), blubber (*F_{bl}*), bone (*F_b*), viscera (*F_v*), and fins (*F_f*); energy densities of blubber (*ED_{bl}*), muscle (*ED_m*), and bone (*ED_b*); and water contents of blubber (%H₂O_{bl}), muscle (%H₂O_m), and bone (%H₂O_b). Energy content of body fluids (blood, interstitial fluids) were ignored. Fluid losses accounted for about 10% of the difference between total weights of undissected specimens and the sum of dissected body fractions.

F_m, *F_{bl}*, *F_b*, *F_v* and *F_f* were determined by measuring the total wet weight of each specimen, and by dissecting the specimen into component parts and weighing each component. Skeletal weight was determined after carefully flensing and scraping all tissue from each bone, including tissue between ribs, between spinal column processes, and within the skull and jaw structures. *ED_{bl}*, *ED_m*, and *ED_b* were determined by bomb calorimetry (Cummins and Wuycheck, 1971). Data used in regressions are means of two or four replicate energy density determinations. Dry weights were determined after freeze-drying samples to constant weight (48 hours) and storing in a desiccator for 24 hours. Ash-free dry weights were determined after ashing samples at 450°C for 4 hours and cooling for 24 hours in a desiccator. Dry and ash-free dry weight determinations were made on samples of 1–20 g wet weight. %H₂O_{bl}, %H₂O_m and %H₂O_b were calculated as

$$(1.0 - (\text{dry weight/wet weight})) * 100.$$

Energy density (*ED_{an}*) of entire dolphins was estimated as the weighted sum of predicted energy densi-

ties of blubber, muscle, viscera, bone, and fins, where weightings were the predicted fractions of total wet body mass for each tissue type. Energy density of viscera was assumed to be the same as energy density of muscle, based on the relatively muscular nature of these organs (compared with bone or blubber) and the absence of any visible fat deposits upon or within organs. Errors were assumed negligible because the viscera comprised a relatively small fraction of total body weight and it appeared unlikely that the viscera represented a major lipid depot in these tropical cetaceans. Energy density of fins was assumed to be the same as energy density of bone, based on the assumption that caloric content of cartilage (the actual composition of fin material) is closer to bone than to either muscle or blubber. Again, errors due to this assumption should be relatively small as the fins contribute

very little to overall body weight. Estimated total energy density is presented as a function of the regression-predicted values of each parameter, where parameter variances are ignored.

Data analysis

Relationships between morphological measurements and total wet weight were determined by using linear regression analysis of log transformed variables, where morphological measurements and wet weights were converted to logarithms (base 10) prior to analysis.

Results

Significant allometric trends ($P < 0.05$) occurred in 23 of the 25 parameters (Table 3; Figs. 2–11). No signifi-

Table 3

Regression equation parameters relating energetics parameters to total wet weight of spotted dolphins (*Stenella attenuata*) from the eastern tropical Pacific Ocean. Regressions performed on log₁₀-transformed data in both X and Y. Re-transformed equation of the form $Y = aX^b$. X units are wet weight in kg. Y units are as noted. Symbols are defined in Table 2.

			n ¹	b ²	se(b) ³	a ⁴	p ⁵
Active metabolism							
D_{max}	(cm)		35	0.294	0.0133	3.17	0.0001
WSA_b	(cm ²)	body	35	0.682	0.006	5.65	0.0001
WSA_{fp}	(cm ²)	flippers	26	0.488	0.022	1.13	0.0001
WSA_d	(cm ²)	dorsal	26	0.543	0.018	1.84	0.0001
WSA_f	(cm ²)	flukes	26	0.598	0.200	0.46	0.0001
MCD_{fp}	(cm)	flippers	26	0.211	0.015	0.14	0.0001
MCD_d	(cm)	dorsal	26	0.299	0.145	0.06	0.0001
MCD_f	(cm)	flukes	26	0.224	0.021	0.14	0.0001
CL_{fp}	(cm)	flippers	26	0.209	0.030	2.08	0.0001
CL_d	(cm)	dorsal	26	0.285	0.015	1.00	0.0001
CL_f	(cm)	flukes	26	0.194	0.019	2.00	0.0001
Passive heat loss (HL_u)							
MSA_b	(cm ²)	body	35	0.729	0.008	2.76	0.0001
BD_a	(cm)	body	29	0.161	0.026	0.14	0.0001
Energy density							
Fractions of body wet weight							
F_{bl}		Blubber	24	-0.247	0.021	0.32	0.0001
F_m		Muscle	24	0.159	0.012	0.32	0.0001
F_v		Viscera	24	-0.153	0.038	0.24	0.0005
F_{bn}		Bone	24	-0.141	0.022	0.12	0.0001
F_f		Fins	22	-0.239	0.034	0.05	0.0001
Energy densities (mJ/kg dry weight)							
ED_{bl}		Blubber	11	0.021	0.007	33.27	0.0178
ED_m		Muscle	9	-0.041	0.013	25.00	0.0132
ED_{bn}		Bone	5	-0.059	0.050	9.12	0.3248
Water content (% of sample wet weight)							
%H ₂ O _{bl}		Blubber	11	-0.289	0.085	316.23	0.0067
%H ₂ O _m		Muscle	10	-0.004	0.007	75.68	0.5956
%H ₂ O _{bn}		bone	5	-0.191	0.023	331.13	0.0141
Estimated Energy Density							
ED_{an}	(mJ/kg wet weight)		35	-0.063	0.000	10.21	0.0001

¹Sample size.

²Estimated slope coefficient.

³Estimated standard error of slope coefficient.

⁴Estimated intercept for fitted regression.

⁵Significance level (probability).

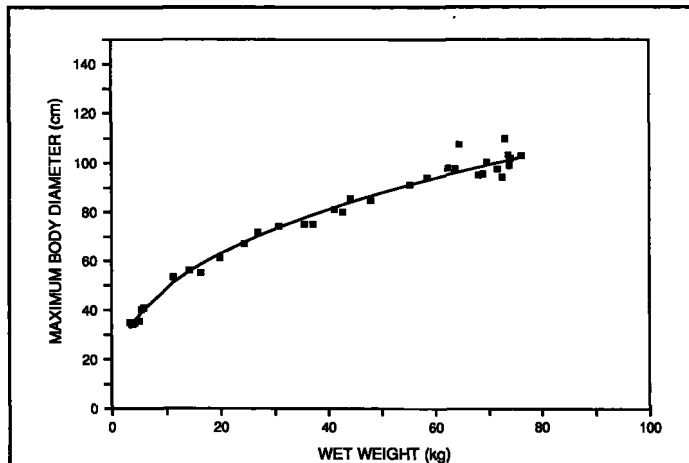


Figure 2

Relationship between **maximum body diameter** (just anterior to dorsal fin; C3 in Fig. 1) and total wet weight of body in kilograms for 35 specimens of spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Solid line is fitted regression.

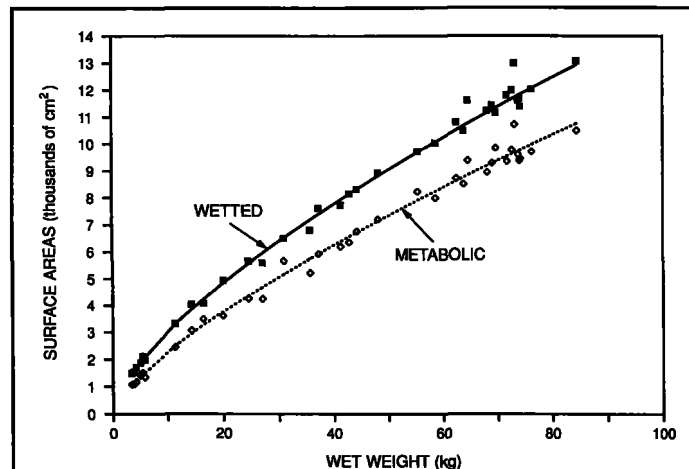


Figure 3

Relationship between **wetted and metabolic surface areas**, and total wet weight of body in kilograms for 35 specimens of spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions.

cant trend was found for $\%H_2O_m$ (Fig. 10) or ED_{bn} (Fig. 9). No trends were isometric (linear) in the untransformed variables. Trends fell into three general groups based on the strength of the relationship between parameter value and wet weight (Table 4). Expressed in terms of the regression coefficient (b), these relationship groups were strong ($0.49 < b < 0.73$), intermediate ($-0.29 < b < -0.14$ or $0.16 < b < 0.30$), and weak ($-0.14 < b < 0.16$). Strong trends were found for all five of the surface area measurements (MSA_b ,

WSA_b , WSA_{fp} , WSA_{db} , WSA_{fl} ; Figs. 3 and 4). Weak trends were found for energy densities of blubber and muscle (ED_{bb} , ED_m ; Fig. 9). Intermediate trends represented the majority of the relationships (16 of 25) and included D_{max} (Fig. 2), all measures of MCD (Fig. 5), CL (Fig. 6), BD_a (Fig. 7), F (Fig. 8, A and B), $\%H_2O_b$ and $\%H_2O_{bn}$ (Fig. 10), and ED_{an} (Fig. 11).

Parameters that exhibited strong trends demonstrated large changes in parameter values throughout the weight range studied. Although the allometric effect decreased somewhat with increasing size, parameter estimates were 300–400% larger for 30-kg than for 5-kg dolphins (compared with a difference of 600% ($30\text{ kg}/5\text{ kg} \times 100$) in wet weight), and 50%–85% larger for 70-kg than for 30-kg dolphins (compared with a difference of 233% in wet weight; Table 4).

Parameters showing intermediate trends changed rapidly only from birth through the first 2–3 years of life (5–30 kg; Perrin et al., 1976; Hohn and Hammond, 1985). Parameter values changed much more slowly with size in older (larger) dolphins (30–70 kg) than in smaller dolphins (e.g., less than 30 kg). For example, estimated muscle fraction of body wet mass increased by 33% from 5-kg to 30-kg dolphins, but only by 14% from 30 to 70 kg wet weight (Table 4). Parameter estimates for these intermediate effects differed from 10% to 70% between 5- and 30-kg dolphins, but only from 5% to 30% between 30- versus 70-kg dolphins (Table 4).

Parameter values showing weak trends changed little with increasing size. For example, estimated ED_m increased only 8% in animals 5 kg to 30 kg in weight, and only an additional 4% from animals 30 kg to 70 kg in weight (Table 4). The lack of any significant trend in ED_{bn} may be due to small sample size ($n = 5$ animals) but the relatively small scatter of the existing points indicates that the apparent absence of trend is probably real (Fig. 9). The lack of trend in H_2O_m also appears real, as sample size was reasonably large ($n = 10$) and scatter about the regression line relatively small (Fig. 10).

Discussion

Estimates for individual dolphins

The practical importance of any allometric trend in any particular parameter will depend not only on the strength of the trend, but also on that parameter's relative contribution to the energy flux being estimated. This contribution is affected by the algebraic placement of the parameter in the energy flux calculation,

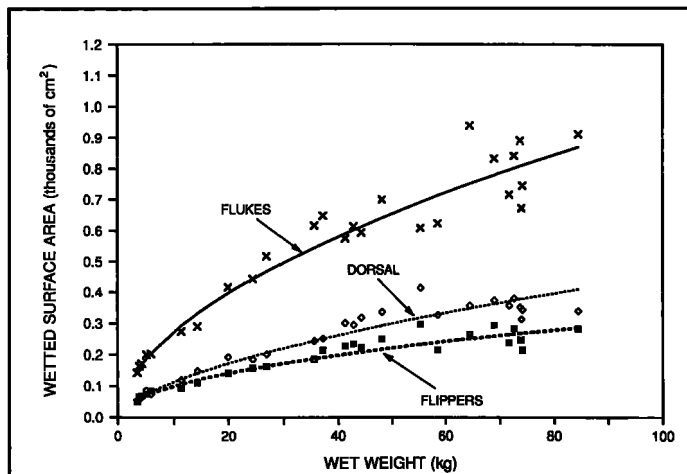


Figure 4

Relationship between **wetted surface areas of fins** and total wet weight of body in kilograms for 26 specimens of spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Areas are total for both sides of dorsal, both sides of both flippers, and both sides of both flukes. Lines through points are fitted regressions.

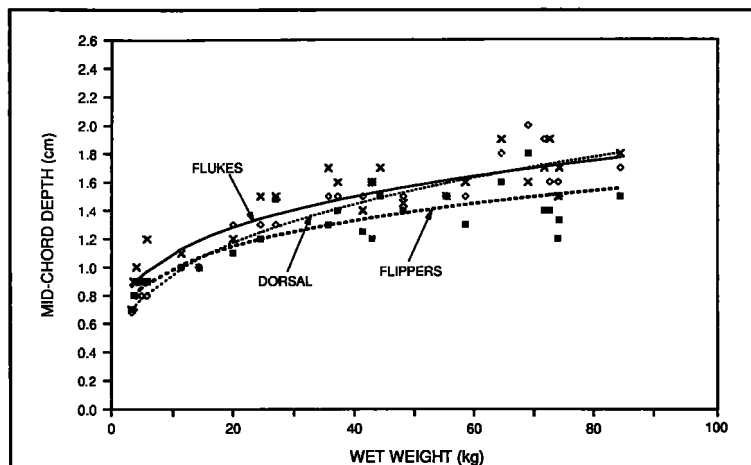


Figure 5

Relationship between **mid-chord depths of fins** and total wet weight of body in kilograms for 26 specimens of spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions.

by the actual values taken on by the parameter, and by the relative importance of the energy characteristic in the overall energy budget.

For example, the relative importance of the parameters WSA_b and D_{max} in the equation for active metabolism is highly dependent on both parameter placement and relationship with wet weight (trend). Active metabolism ($\text{cal}\cdot\text{hr}^{-1}$) can be estimated for steady submerged swimming by torpedo-shaped bodies as

$$ACT = 20650 * MP / (ME * PE),$$

where $ME = 0.20$

$$PE = 0.85$$

$$MP = ((D_T / 1e^7) * VL)$$

$$D_T = (0.5 * N * VL^2 * WSA_b * C_T) / (1.0 - FID)$$

$$N = (1.025 \text{ g/cm}^3)$$

$$FID = 0.21$$

$$C_T = C_f * [1 + (1.5 * ((D_{max} / TL))^{3/2} + (7 * ((D_{max} / TL))^3)]$$

$$C_f = 0.072 R_L^{-1/5}$$

$$R_L = (TL * VL) / \nu$$

$$\nu = 0.01 \text{ Stokes}$$

VL is velocity ($\text{cm}\cdot\text{sec}^{-1}$) and TL is total length in centimeters (Edwards, 1992, following Webb, 1975).

Collecting and assuming constant all terms except the energetics parameters WSA_b and D_{max} , the expression for active metabolism can be simplified to

$$ACT = C * WSA_b * [1 + (1.5 * ((D_{max} / TL))^{3/2} + (7 * ((D_{max} / TL))^3)],$$

where C represents the collected terms.

The effects of increasing or decreasing the values used for WSA_b and D_{max} can be seen more readily in this formulation. Changes in the value of WSA_b lead directly to equivalent changes in the estimate of ACT (e.g., increasing WSA_b by 50% will increase the estimated cost of activity by 50%). WSA_b not only has a direct effect on estimates of activity cost, but has also a strong relationship with wet weight, leading to differences of up to 80% in estimates of activity costs for 30-kg versus 70-kg spotted dolphins (WSA_b for a 70-kg dolphin is 78% larger than for a 30-kg dolphin, Table 4). Differences are near 350% for 5-kg versus 30-kg dolphins (WSA_b for a 30-kg dolphin is 339% greater than for a 5-kg dolphin, Table 4).

Conversely, changes in D_{max} have little actual effect on activity estimates, both because changes with size are smaller overall and because of the parameter's algebraic placement in the equation for activity costs. The ratio D_{max} / TL will always be quite small (e.g., $5/80 = 0.065$ in an 80-cm dolphin ($D_{max} = 5$ cm) weighing 5 kg; $11/210 = 0.052$ in a 210-cm dolphin ($D_{max} = 11$ cm) weighing 70 kg). Because this small term is made even smaller by raising it to higher powers, changes in D_{max} will have little effect on estimates of ACT (e.g., doubling D_{max} from 5 to 10 cm for an 80-cm dolphin

changes the value of the term in brackets only from 1.03 to 1.08). This lack of effect occurs despite the fact that D_{max} has an intermediate-level relationship with wet weight (Table 4).

Examining the placement of MSA_b and BD_a in the equation for passive heat loss also illustrates that their relative importance is highly dependent on both parameter placement and relationship with wet weight. Passive heat loss can be estimated as (Edwards, 1992, following Brodie, 1975).

$$H_u = \frac{((21.18/BD_a) * (37.0 - T_a) * MSA_b / 10000.0) * 24}{WW_g * (CD_d / 1000.0)}$$

Collecting and assuming constant all terms except the energetics parameters BD_a and MSA_b ,

$$H_u = (MSA_b / BD_a) * C,$$

where C represents the collected terms.

Once again, changes in the surface area measurement (MSA_b) will lead directly to equivalent changes in estimates of HL_u , and the strong relationship between MSA_b and wet weight will be readily reflected in the estimates. However, unlike the case for D_{max} , changes in values used for BD_a will have a significant (reciprocal) effect on estimates of HL_u (e.g., increasing blubber depth by 30% [i.e., by a factor of 1.30] will decrease the estimate for H_u by about 23% [$1/1.30 = 0.77$]) owing to the difference in the way the parameter is expressed in the equation. In this case, the intermediate-level relationship of BD_a with wet weight will be reflected in the estimate of energy flux.

Allometric effects in parameters related to bone provide an example of largely irrelevant, though statistically significant, trends. The bone fraction of body weight is small (about 10%: Fig. 8A), and its energy density low (less than 1/4 the energy density of blubber, 1/3 the energy density of muscle). Given no indication from the energy densities in the small sample studied that spotted dolphins store lipid within the skeleton, even relatively large changes with size will have little effect on whole-animal energy calculations. Even though the fraction of body weight due to bone has an intermediate-level relationship with wet weight, decreasing 30% from 5-kg to 30-kg dolphins, the decrease in terms of total body weight is only from 10% to 7% (Table 4).

Thus, the practical importance of any allometric trend depends on other factors in addition to actual strength of the trend with wet weight, but in general for spotted dolphins, these trends are expressed primarily during the first two or three years of life (5-30 kg wet weight). Parameter estimates for small

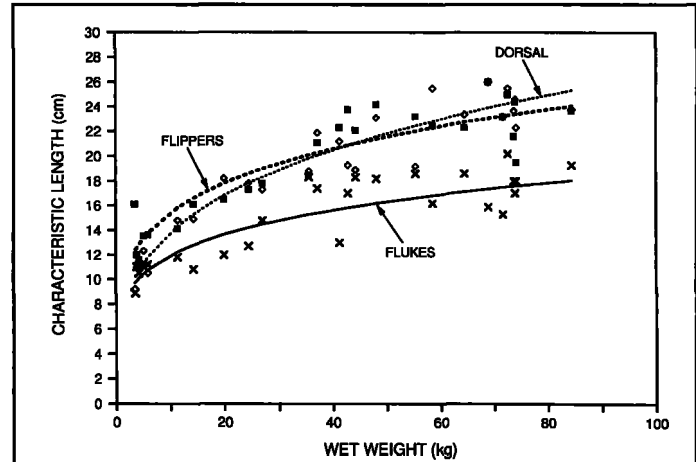


Figure 6
Relationship between characteristic lengths of fins and total wet weight of body in kilograms for 26 specimens of spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions.

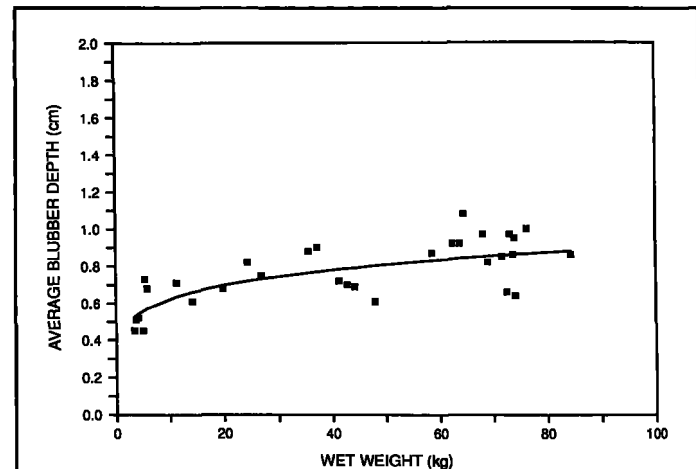
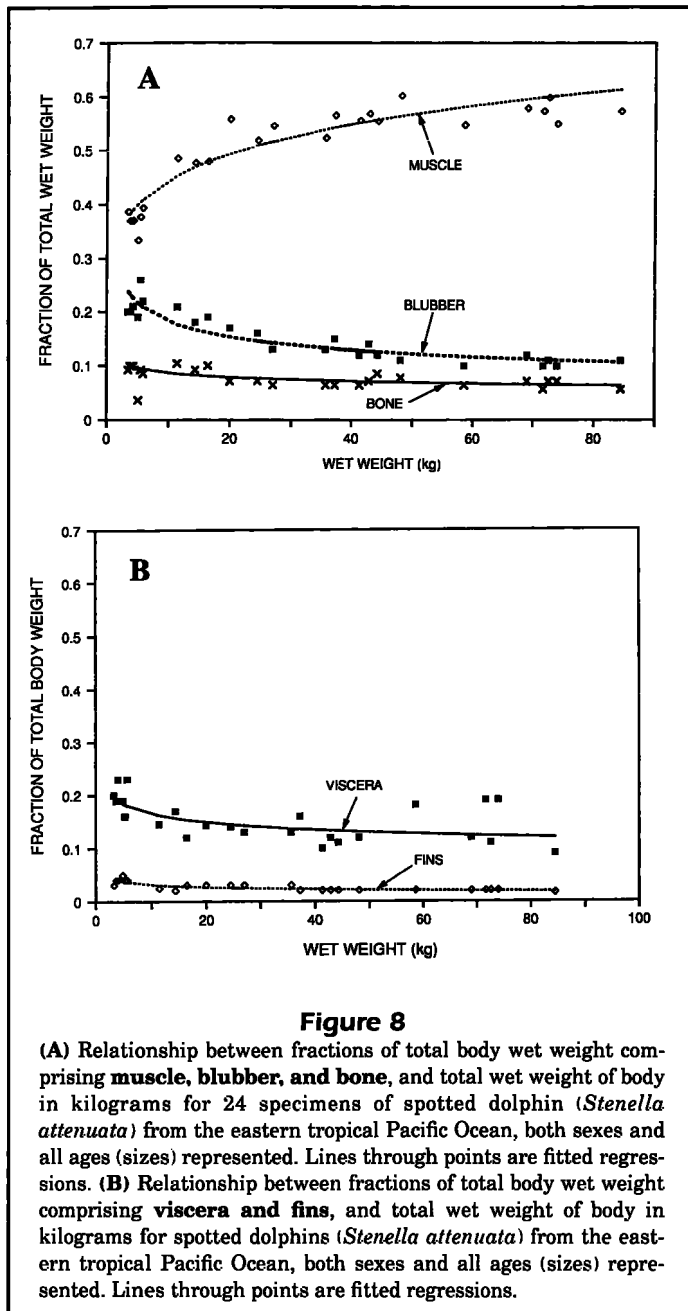


Figure 7
Relationship between average blubber depth and total wet weight of body in kilograms for 29 specimens of spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions.

dolphins (less than about 30 kg wet weight) should be derived from measurements on animals near the specific size of interest. Estimates for larger animals, with the exception of the surface area measurements, could be estimated reasonably well from any specimens greater than about 30 kg wet weight.

Population energetics

The examples presented above pertain to estimates for individual spotted dolphins. Implications of allo-



metric trends for estimates of population energy flux are not necessarily straightforward. Dolphins less than about 3 years old represent only about 10% of the population in these relatively long-lived and slowly reproducing mammals; dolphins age 3–12 compose about 40% and sexually mature adults about 50% of the population (Barlow and Hohn, 1984; Hohn and Hammond, 1985). Because they are so few and because their biomass is so small, ignoring allometric effects when estimating energy fluxes for the younger animals, or ignoring the younger animals altogether,

will have little direct effect on population energy budgets.

However, the indirect effects may be considerable. To the extent that activities of older animals are constrained by energy-related characteristics of young dolphins, indirect effects of size-related differences in estimated energy fluxes may be more important than the absolute fluxes themselves, through regulating behavior or ecological relationships. For example, muscle fraction of body mass in neonate dolphins (5 kg) is about 30% less than the muscle fraction in adults (70 kg; Figure 8A, Table 4). Thus the power available for swimming (as a function of muscle mass) is 30% less than would be estimated based on measurements from adult animals. The estimated speeds that small dolphins, with their smaller muscle mass, can maintain will be slower than speeds estimated by simply applying to neonates parameter values derived from adults.

Differences in estimated swimming speed may be important because dolphins are schooling mammals with apparently strong social ties and prolonged periods of parental care for nursing offspring. In order to remain within the same school, the average speed for all individuals will be constrained to the slower speeds that can be maintained by smaller dolphins. Estimates from tagging studies of spotted dolphins in the ETP indicate that in fact the average cruising speed of dolphin schools is the optimum for neonates rather than for adults, despite the fact that adults represent the majority of individuals in the schools (Edwards, 1992, and references therein). Using parameters appropriate for adult dolphins in estimates for the smaller animals would produce unreasonably high estimates of sustainable power output (and therefore food consumption) by the smaller animals (Edwards, 1992). School speeds, and therefore energy requirements to maintain these speeds, may thus be constrained by energetics characteristics of small animals that cannot be extrapolated simply from measurements on adults. As cost of transport is a large fraction of the total energy requirements of a swimming mammal (active metabolism in swimming homeotherms [including dolphins, sea otters, and penguins] is generally 2 to 3 times that of resting metabolic rates [Hui, 1987]), maintaining reduced speeds should reduce energy costs and therefore forage requirements for the school moving as a unit. This is particularly significant because forage requirements are the most commonly estimated energy flux used to estimate the impact of a

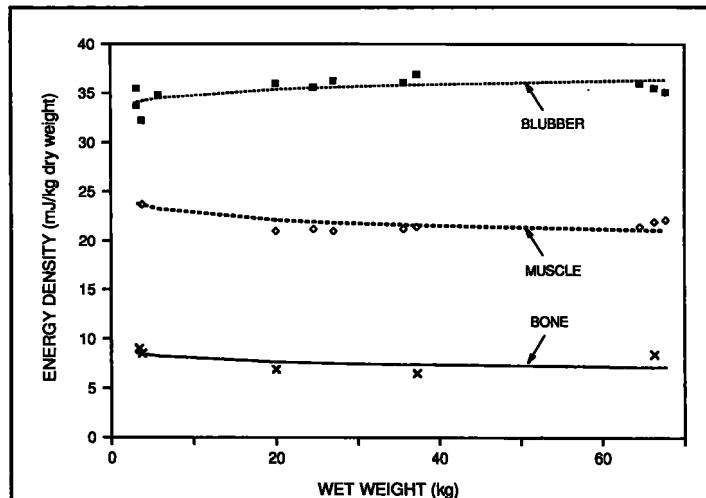


Figure 9

Relationship between energy density (per gram dry weight) of blubber (11 specimens), muscle (9 specimens) and bone (5 specimens), and total wet weight of body in kilograms for spotted dolphins (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions.

Table 4

Predicted values and fractional differences (ratios) between those values for energetics parameters showing strong, intermediate, and weak allometric effects, for spotted dolphins weighing 5, 30, and 70 kg wet weight. Regression coefficient indicated by (b).

	Predicted values			Ratios	
	5 kg	30 kg	70 kg	30 kg/5 kg (6.0)	70 kg/30 kg (2.3)
Strong relationship ($b > 0.49$)					
MSA_b	8.92	32.94	61.09	3.69	1.85
WSA_b	16.93	57.47	102.42	3.39	1.78
WSA_{fp}	2.48	5.94	8.98	2.40	1.51
WSA_d	4.41	11.67	18.48	2.65	1.58
WSA_f	1.20	3.52	5.84	2.92	1.66
Intermediate relationship ($-0.14 < b < -0.29$ or $0.16 < b < 0.30$)					
D_{max}	5.09	8.62	11.05	1.69	1.28
MCD_{fp}	0.20	0.29	0.34	1.46	1.20
MCD_d	0.10	0.17	0.21	1.71	1.29
MCD_f	0.20	0.30	0.36	1.49	1.21
CL_{fp}	2.91	4.23	5.05	1.45	1.19
CL_d	1.58	2.64	3.36	1.67	1.27
CL_f	2.73	3.87	4.56	1.42	1.18
BD_a	0.20	0.26	0.29	1.29	1.13
F_{bl}	0.22	0.14	0.11	0.64	0.81
F_m	0.41	0.55	0.63	1.33	1.14
F_v	0.19	0.14	0.13	0.76	0.88
F_{bn}	0.10	0.07	0.07	0.78	0.89
F_f	0.03	0.02	0.02	0.65	0.82
H_2O_{bl}	198.61	118.34	92.63	0.60	0.78
H_2O_{bn}	243.50	172.93	147.09	0.71	0.85
ED_{an}	9.23	8.24	7.81	0.89	0.95
Weak or insignificant relationship ($-0.29 < b < 0.16$)					
ED_{bl}	34.41	35.73	36.37	1.04	1.02
ED_m	23.40	21.75	21.00	0.93	0.97
ED_{bn}	8.29	7.46	7.10	0.90	0.95
$\%H_2O_m$	75.19	74.66	74.40	0.99	1.00

cetacean population preying on a fisheries resource (e.g., Overholz et al., 1991).

The practical significance of these results for a given population's estimates will depend on values chosen for a number of parameters in addition to those presented here (e.g., ambient temperature, average swimming speed, size composition of the population). Such calculations are beyond the scope of the present study, but these results for spotted dolphins from the ETP show that allometric trends should be considered in such calculations. Similar effects probably occur in other cetacean populations and should be investigated.

Caveats

The regressions presented here include data from a number of "neonate" dolphins which were actually late-term fetuses rather than true neonates. Specimens of true neonates are rare. But the relatively smooth fit through data collected from near-term fetuses and first to third-year juveniles imply that the physical characteristics predicted for the under-sampled size ranges from 5–30 kg wet weight, if one uses the regressions presented here, are likely to be accurate.

The large water content of bone and blubber in fetal specimens probably reflects conditions that change rapidly after birth, when fetal nutrition changes from placental to milk-derived. It is not possible with the present data set to identify exactly how quickly water content decreases. However, errors in energetics estimates resulting from inaccurate estimates of bone water content will be negligible owing to the relatively small contribution made to energy flux by skeletal materials. Errors in estimates of water content of blubber for spotted dolphins in the weight range 5–30 kg wet weight could be more serious. Although the true extent of the problem cannot be determined from this data set, possible values for this size range vary from about 15% to 30% (Fig. 10).

Changes in maternal body composition (and thus energetics estimates) during pregnancy and lactation may occur in spotted dolphins as they do in large whales (Lockyer 1981, a and b) but such changes, if they occur, are apparently much more subtle in spotted dolphins from the ETP. No dramatic differences in body fractions or energy density of blubber or muscle were discernable in the set of specimens analyzed during this study, which were collected from a variety of times and places. It is unlikely that major changes occur in

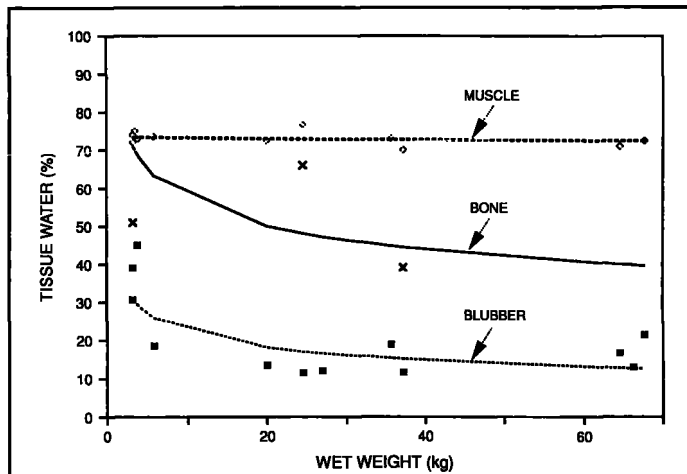


Figure 10

Relationship between **water content** of muscle, blubber and bone vs. total wet weight of body in kilograms for spotted dolphins (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented. Lines through points are fitted regressions.

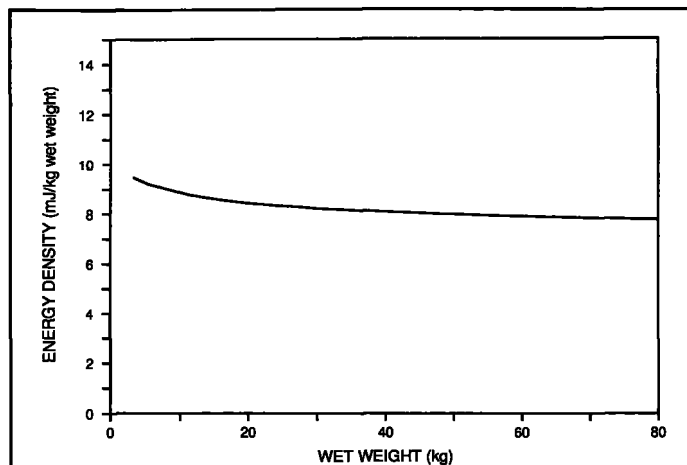


Figure 11

Estimated relationship between **total energy density** and total wet weight of body in kilograms for spotted dolphin (*Stenella attenuata*) from the eastern tropical Pacific Ocean, both sexes and all ages (sizes) represented.

spotted dolphins, as these small cetaceans appear to reside continually within the *relatively* constant (compared to temperate and polar regions) environment of the eastern tropical Pacific Ocean (Fiedler, 1990). There is apparently little need for these animals to develop and sequester significant energy reserves and insulation for conducting lengthy migrations to or through areas of little food, or through areas of cold water.

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