

BACULAR SIZE, GROWTH, AND ALLOMETRY IN THE LARGEST EXTANT OTARIID, THE STELLER SEA LION (*EUMETOPIAS JUBATUS*)

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Bacula are relatively small in terrestrially mating species of pinnipeds (otariids and elephant seals, *Mirounga*), perhaps reflecting adaptive size reduction to minimize bacular fracture. Fur seals and sea lions (Otariidae) are a good group with which to investigate this question, because most species copulate solely on land and body size varies interspecifically. We studied bacular size and relative growth in the largest extant otariid, the Steller sea lion (*Eumetopias jubatus*). Bacula roughly tripled in length and increased 30-fold in mass between 1 and 8 years of age. Allometric relationships changed over development; bacular length and mass changed from being initially positively allometric to body length to negatively allometric and isometric, respectively; bacular mass and thickness were positively allometric to body length throughout life, and apical growth was isometric then was positively allometric to bacular length. In adults (>7 years of age), bacula averaged 18.1 cm length (6.2% of body length), 36.7 g mass, and 2.02 g/cm density (mass:length). The baculum of *Eumetopias* is about the same length relative to body length as in other adult male otariids but is about twice the density, presumably to increase strength. Information on small or aquatically mating species of otariid are needed to extend our findings and interpretations.

Key words: allometry, baculum, character variation, *Eumetopias jubatus*, growth, sexual selection

Pinnipeds have diverse patterns of life history, sexual dimorphism, and mating systems, so reproductive competition and success have been studied extensively (Bartholomew 1970; Boness 1991; Le Boeuf and Reiter 1988; Stirling 1983). As for other mammals however, surprisingly little attention has been given to the likely important roles of sperm competition or cryptic female choice in sexual selection (Eberhard 1985, 1996, 1998; Gomendio et al. 1998). These forms of intra- and intersexual selection have led to numerous and diverse behavioral, physiological, and anatomical adaptations in animals, some of which also must occur in pinnipeds.

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Bacula of pinnipeds have received some attention in this regard (Dixson 1995; Scheffer and Kenyon 1963). Bacula are relatively large in phocids and relatively small in otariids, a pattern that seems attributable to 3 selective forces (Miller et al. 1998, 1999; Oosthuizen and Miller 2000). First, multiple mating within single breeding seasons is ubiquitous in female phocids (Atkinson 1997; Le Boeuf 1972; Perry and Amos 1998), so sperm competition must occur, leading in turn to adaptations for displacement of competitors' sperm or deep insertion, for which a voluminous or long penis would be advantageous. In contrast, female otariids usually only mate once per

year (Boness 1991; Gentry 1998), so sperm competition must be relatively weak. Second, water can damage sperm, so long intermittent organs have arisen independently in various animal groups in which aquatic mating occurs (Briskie and Montgomerie 1997). Phocids have relatively larger testes than otariids, which is consistent with the hypothesis that the intensity of sperm competition differs between the 2 families (Miller et al. 1998, 1999; Oosthuizen and Miller 2000). Finally, large strong bacula may be selected for in species that copulate aquatically; animals have great freedom of movement in water, so bacula could be fractured during violent copulations, for example if a copulating male is attacked.

The latter interpretation is supported by exceptions to the widespread difference in bacular size between phocids and otariids in the largest extant pinnipeds; the terrestrially mating elephant seals (*Mirounga angustirostris* and *M. leonina*) have a small baculum, and the aquatically mating walrus (*Odobenus rosmarus*) has a large one (Dixon 1995; Fay 1982; Laws 1956; Mohr 1963; Scheffer and Kenyon 1963). Therefore, bacular size may be evolutionarily constrained in large terrestrially mating species due to the risk of bacular fracture.

The largest extant otariid is the Steller sea lion (*Eumetopias jubatus*), adult males of which can exceed 3 m in body length and 1,000 kg in mass (Loughlin et al. 1987). In contrast, adult males of the smallest otariid (Galápagos fur seal, *Arctocephalus galapagoensis*) average only about 150 cm in body length and 65 kg in mass (Reeves et al. 1992; Reppenning et al. 1971). *Eumetopias* has a typical otariid breeding system, with territoriality among adult males and terrestrial copulations (Gentry 1970, 1975; Loughlin et al. 1987).

We studied the baculum of *Eumetopias* and compared its growth and relative size with other species of otariids. We included measurements on the bacular apex in the study, because apical anatomy varies across otariid species (Kim et al. 1975; Morejohn

1975), and apical size and shape may be perceptible to female otariids during copulation (see Discussion).

MATERIALS AND METHODS

Specimens ($N = 103$) in the collection of the National Marine Mammal Laboratory were used for this study. Most specimens were collected in Alaska in the 1950s and 1970s (Calkins and Pitcher 1982; Pitcher and Calkins 1981; Thorsteinson and Lensink 1962). The collection included some animals found dead. We examined an unknown proportion of bacula collected by Thorsteinson and Lensink (1962) and studied by Fiscus (1961), making it difficult to compare our findings with those studies. We remeasured the single specimen reported by Scheffer and Kenyon (1963).

Standard length (American Society of Mammalogists 1967) was used as a measure of body size for this study, because body mass of pinnipeds is highly variable. Specimens were aged by counting annuli in canines or postcanines. For the former, 1 lower canine was cut parasagittally with a band saw. The large half-section was then polished and (usually) etched with 5% formic acid for 1–2 h; dentinal layers were counted as annual lines (Fiscus 1961; Perrin and Myrick 1980; Scheffer 1950a; Spalding 1964). Alternatively (Calkins and Pitcher 1982), one 2nd upper postcanine was decalcified, sectioned at about 48 μm and stained with hematoxylin; ages were estimated from cementum annuli. The annual deposition of cementum annuli was confirmed by sectioned teeth from 9 specimens of known age (branded as pups). Median birth date was set at 13 June (T. R. Loughlin, in litt.); based on that date, age was estimated to the nearest 0.1 yr.

Some specimens ($N = 16$) had an unknown collecting date, but known age class. Animals in their n th year of life were considered to be of age class n , so that ages of specimens with unknown collecting dates (all in age classes >7) were estimated to the nearest one-half year as $n - 0.5$. Data on age, collection date, or standard length were not available for all specimens, and some bacula were broken, so sample sizes varied for our analyses.

McLaren (1993) experienced some difficulty in estimating asymptotic growth in this species and noted high variation in body size of adults.

In the present study, we used means for males >7 years of age as asymptotic estimates.

Measurements were taken on the following bacular variables: 1) mass, 2) length, maximal 3) height and 4) breadth near proximal end, 5) height and 6) breadth midway along shaft, and 7) height and 8) breadth of apex. Mass was estimated to the nearest 0.1 g with an electronic balance, and linear measurements were estimated to the nearest 0.1 mm with digital calipers. "Density" per unit length was computed as mass: length. To reduce measurement error, because torsion was common near the proximal end of the baculum, and to provide an overall estimate of bacular thickness, measurements on variables 3–6 were summed for allometric analyses. The ratio of apical height to breadth was not related to body length or age, so measurements on those 2 variables also were summed for analysis.

Reduced major axis or geometric mean regression (GMR) is generally preferable to simple linear regression (SLR) in allometric studies because there is no distinction between explanatory and response variables and because all variables are measured with error (Harvey and Harcourt 1984; McLaren 1993; Teissier 1960). These 2 kinds of regression are identical when $r = 1$ because in GMR, slope = b/r , where b is the slope in SLR (Ricker 1975). Thus, for practical purposes, SLR is often acceptable for allometric analysis, and it has the desirable property of being statistically well known. For allometric analyses of body parts relative to overall body size, it also is reasonable to use SLR (Teissier 1960). GMR is normally more suitable for analyses involving body parts, and we used it for that purpose. For the reasons given, however, and because SLR is used so widely (Dawson 1994; Gould 1966), we also present SLR slopes and intercepts. Estimates of slopes, intercepts, and CI are provided (Peters 1983).

Relationships between variables were not linearized by log-log transformations over the whole size range, although linearity in 2 cases was reasonably well approximated (bacular mass versus bacular length; basal + shaft diameters versus bacular length). Therefore, 2 or 3 allometric analyses were carried out for each pair of variables to describe allometric relationships adequately. Data on specimens known or presumed to be ≥ 1 year of age were used, which excluded only 4 young (all <1 month of age).

Points for dividing each data set were determined by visual inspection of bivariate log-log plots. Allometric analyses were based on size rather than age, to increase sample sizes and because small and large individuals of the same age (especially early in life and during sexual maturation) distorted allometric relationships due to growth.

Data and statistical results were reported to 3 decimal places for values <1, to 2 decimal places for values <10, to 1 decimal place for values <100, and with no decimal places for higher values. Standard deviations are given with 1 more decimal place than their associated means (Sokal and Rohlf 1981). Some specimens in the present study were from the collection of Thorsteinson and Lensink (1962) and also were reported by Fiscus (1961) (see Table 1, footnote 2). Analyses were carried out with Kaleidagraph 3.0 (Abelbeck Software, Reading, Pennsylvania) and Statview 5.0 (SAS Institute Inc., Cary, North Carolina).

RESULTS

Body and bacular growth were rapid and stabilized after about 7 years of age (Fig. 1). Early growth in bacular mass, density, and thickness was slower than in body and bacular length, then increased sharply and was rapid through the period of sexual maturation (Figs. 1C–F). Sample sizes of young males were too small to quantify pubertal growth, but it was apparent that greatest bacular growth took place over years 5–7. Between years 1 and 8, bacular length roughly tripled, and bacular + shaft diameters and apical diameters roughly quadrupled; bacular mass increased about 30-fold (Figs. 1B–F). Descriptive statistics on absolute and relative body length and on bacular variables for males >7 years of age are summarized in Table 1.

Growth differences between variables led to varied patterns of relative growth. Allometric analyses for different size ranges are summarized in Table 2. Analyses revealed positive allometry of bacular length (Fig. 2A), mass (Fig. 2B), and density relative to body length in small specimens and negative allometry (bacular length; Fig. 2A) or

TABLE 1.—Summary of descriptive statistics on body and bacular size for male Steller sea lions >7 years of age.

Variable	Mean	SD	Range	N
Body length (cm)	293 ^a	22.6	251–330	20
Bacular length (cm)	18.1	1.02	15.6–20.0	22
Bacular length : body length (%)	6.24	0.518	5.12–7.08	19
Bacular mass (g)	36.7 ^b	9.30	23.6–55.1	22
Bacular density (g/cm)	2.02	0.428	1.38–2.75	22
Basal height + breadth (mm)	48.8	6.12	37.2–59.0	23
Basal height (mm)	23.2	3.51	15.7–28.8	23
Basal breadth (mm)	25.5	3.18	20.5–31.0	23
Midshaft height + breadth (mm)	27.6	2.93	22.2–32.8	21
Midshaft height (mm)	14.7	1.49	12.4–17.2	22
Midshaft breadth (mm)	13.0	1.63	9.70–16.6	21
Apical height + breadth (mm)	42.4	2.73	37.0–48.9	21
Apical height (mm)	23.5	2.02	19.7–26.2	22
Apical breadth (mm)	18.9	2.05	16.5–23.0	21

^a Based on data for 65 and 35 males >3 years of age from, respectively, the Gulf of Alaska and Shelikof Strait, Alaska; McLaren (1993) estimated asymptotic standard lengths as 293 and 296 cm. Some specimens in our study were used in his analyses.

^b For 114 males >8 years of age collected from Ugamak to Marmot Islands, Alaska, mean mass (mean of age-class means) = 38.9 g (range 25–54—Thorsteinson and Lensink 1961). Some specimens in the present study were from the collection of Thorsteinson and Lensink (1962). For the same specimens, Fiscus (1961) reported maximal mass as 54.6 g from a 16-year-old male.

isometry (bacular mass and density; Fig. 2B) relative to body length in large specimens.

More diverse patterns characterized relative growth of bacular variables. Both bacular mass and basal + shaft diameters exhibited positive allometry relative to bacular length, and that was stronger in large than in small specimens (Fig. 2C). Isometry characterized early growth of the apex relative to bacular length, which was followed by strong positive allometry (GMR slope = 1.19 in small, versus 2.66 in large, specimens; Fig. 2E). There was a suggestion of slower growth of the apex relative to bacular length for long bacula, but the pattern was indistinct because of the small size range represented (Fig. 2E). Basal + shaft diameters had a roughly sigmoidal relationship to apical diameters (Fig. 2F); isometry and weak negative allometry characterized small and large specimens, respectively, and strong positive allometry (GMR slope = 2.64) characterized the intermediate size range.

DISCUSSION

Relative bacular size.—The baculum of *Eumetopias* was described by Pohl (1911),

Chaine (1926), Mohr (1963), and Morejohn (1975). Burt (1960) also described a baculum of this species but misattributed it to the California sea lion, *Zalophus californianus* (Mitchell 1966; Morejohn 1975). Measurements on adult specimens by Morejohn (1975) included 2 specimens with 24- and 25-mm apical breadths, which exceeded our observed maxima. All other published measurements for adult bacula are within ranges we observed for animals >7 years of age. Estimates of bacular mass by Thorsteinson and Lensink (1962) exceed ours by about 6% (Table 1, footnote 2). Their sample was of territorial males only, so for young males, it was likely biased toward animals that were large for their age (Roberts 1988; Scheffer 1950b). Additionally, Alaskan *Eumetopias* averaged larger in body size in 1958 than in the 1970s (Calkins et al. 1998).

In our study, bacular length averaged 6.2% of body length in animals >7 years of age (mean body length = 293 cm). Only 1 estimate is available for other adult sea lions: 6.8% for 1 *Zalophus* (body length = 177 cm—Scheffer and Kenyon 1963). Other estimates for adult otariids are 7.4% for

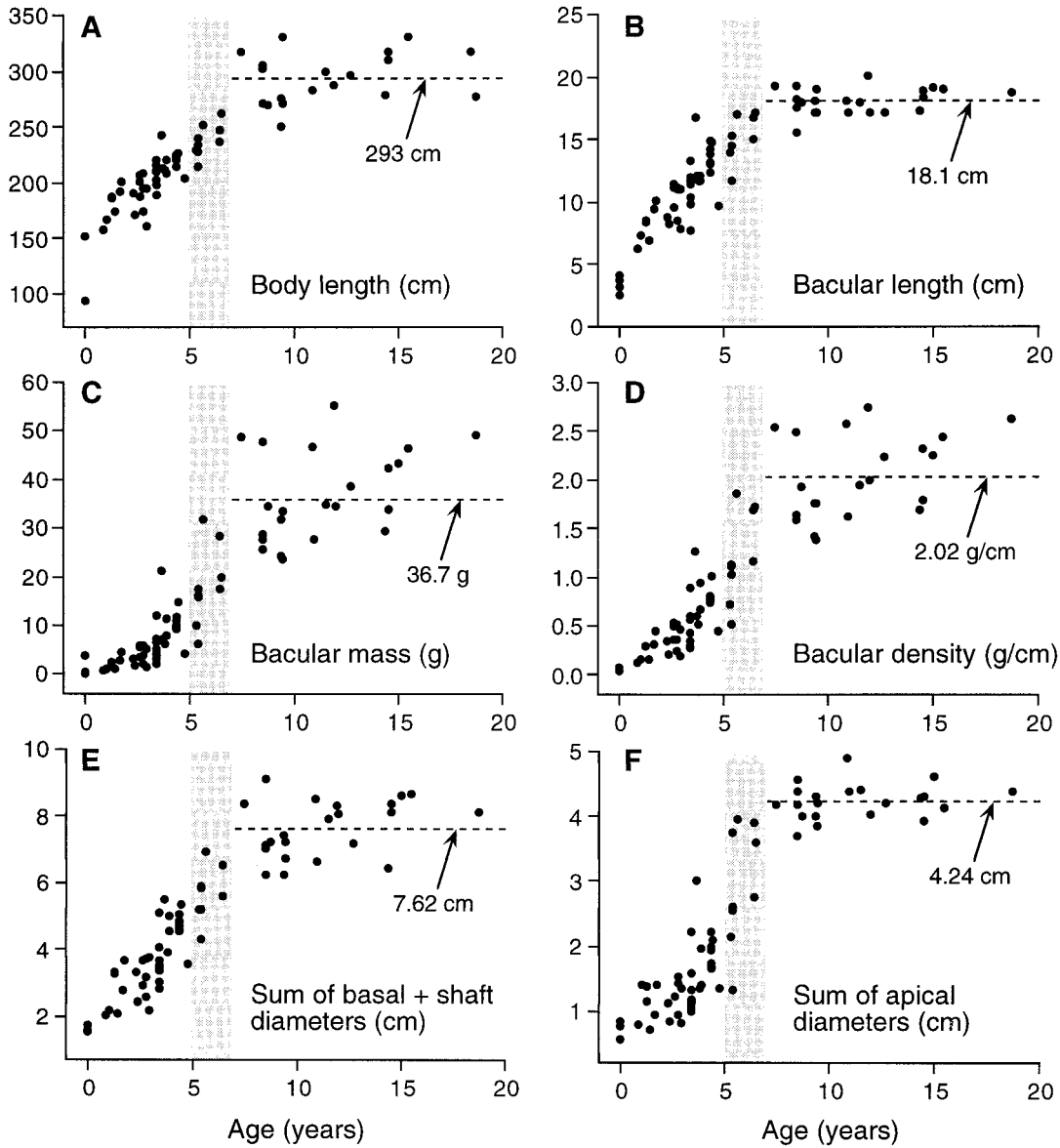


FIG. 1.—Change with age in A) body length, B) bacular length, C) bacular mass, D) bacular density, E) basal plus shaft diameters, and F) apical diameters in male Steller sea lions. Some 3- and 4-year-old males exhibit spermatogenesis, but most do so between 5 and 7 years of age (Calkins and Pitcher 1982; Perlov 1973; Pitcher and Calkins 1981); the latter range is highlighted by a gray rectangle. The dashed lines indicate mean values for males >7 years of age.

1 northern fur seal (*Callorhinus ursinus*, body length = 193 cm—Scheffer and Kenyon 1963) and, for large samples, 6.8% for Cape fur seal (*Arctocephalus pusillus pusillus*, mean body length = 186 cm—Oosthuizen and Miller 2000) and 5.9% for sub-

Antarctic fur seal (*A. tropicalis*, mean body length = 163 cm—Bester 1990). Relative bacular length, therefore, seems to be uniform in otariids, although the range of body sizes represented is not great. Information on bacular size in the small Galápagos fur

seal and in populations or species in which aquatic copulation is common (Juan Fernández fur seal, *A. philippii*—Francis and Boness 1991) would be valuable.

Bacular size may be decoupled from body size if the baculum has functions other than just mechanical support (Patterson 1983). In sciurids, bacular and body size are not correlated with one another, and the bacular apex is complex—presumably to stimulate the female's reproductive tract or displace competitors' sperm (Patterson 1983; Patterson and Thaler 1982). In contrast, the baculum serves only as a supporting rod in many murids, and size is coupled with body size (Patterson 1983). The situation in pinnipeds may be similar because otariids and phocids differ in proximity of the apex to the glans and in apical complexity. In otariids, mechanical support is an important function of the baculum (Miller et al. 1996); however, the bacular apex lies close beneath the glans, so size and shape are probably perceptible to the female during copulation (Green 1972; Harrison 1969; Harrison et al. 1952; Laws and Sinha 1993; Tedman 1991). The apex also is morphologically complex and differs across species (Morejohn 1975). In contrast, the bacular apex of phocids is deeper within the penis, is anatomically simple, and shows little interspecific variation, so the phocid baculum may function mainly for mechanical support. Therefore our observation that bacular and body size in otariids are not correlated interspecifically agrees with Patterson's (1983) hypothesis.

We estimated density of bacula as 2.0 g/cm in adult *Eumetopias*, which is much higher than in other adult otariids: 0.9 g/cm for 6 *Zalophus* (Mohr 1963; Scheffer and Kenyon 1963), 0.8 g/cm for 2 southern sea lions (*Otaria byronia*—Mohr 1963), and for large samples, 0.7 g/cm for *A. p. pusillus* (Oosthuizen and Miller 2000) and 0.7 g/cm for *Callorhinus* (E. H. Miller, in litt.). Bacular density in *Eumetopias* is thus higher than in other otariids and is similar to values for adults of 2 well-studied phocids:

2.8 g/cm in harp seals (*Pagophilus groenlandicus*—Miller et al. 1998) and 2.1 g/cm in hooded seals (*Cystophora cristata*—Miller et al. 1999). Data in Mohr (1963) and Scheffer and Kenyon (1963) suggest that bacula are usually more dense in phocids than otariids. Bacular density in the large terrestrially mating northern elephant seal (*M. angustirostris*) is higher than in *Eumetopias* (3.6 and 3.9 g/cm in adults—Mohr 1963; Scheffer and Kenyon 1963, respectively), but even higher values occur in some aquatically mating species of phocids (E. H. Miller and J. J. Burns, in litt.), and an extraordinarily high density of about 16 g/cm occurs in the aquatically mating walrus (Fay 1982).

In summary, bacular length relative to body length is about the same in *Eumetopias* as in other, smaller otariid species, but bacular density is much higher in *Eumetopias*. Higher density may be an adaptation to increase bending strength and resistance to fracture, although this interpretation is offered cautiously because of the complicated and poorly documented relationships among bacular density, bacular length, body size, mating behavior (aquatic versus terrestrial), and skeletal density in relation to diving behavior in pinnipeds.

Allometry.—Pairwise allometric plots between bacular variables and body length and among bacular variables were not linear in our study. In animals, nonlinear relationships typically result from major developmental events such as metamorphosis and are otherwise unusual (Klingenberg 1998). Such relationships seem to be usual for pinniped bacula. For example, Fay (1982) distinguished 4 phases in relative growth of bacular mass:bacular length in *Odobenus*, with allometric relationships differing among phases. High growth occurred from 0 to 3 months of age (allometric slope in SLR = 4.9), slower growth in juveniles 1–2 years of age (slope = 1.8), more rapid growth in preadolescent and adolescent animals 3–10 years of age (slope = 3.2), and the most rapid growth (slope = 5.0) in sub-

TABLE 2.—Summary of allometric (log-log) regressions for Steller sea lions >1 year of age. Results from simple linear regression (SLR) and geometric mean regression (GMR) are shown, as appropriate.

Log Y versus log X variable	Range of X variable	Allometry ^a	SLR or GMR	Slope (95% CI)	Intercept (95% CI)	P	R ²	N
Bacular length (cm) versus body length (cm)	<241 cm	+	SLR	2.10 (1.87, 2.32)	-3.80 (-4.32, -3.28)	<0.0001	0.89	44
Bacular length (cm) versus body length (cm)	>242 cm	-	SLR	0.407 (0.149, 0.666)	-0.254 (-0.380, 0.888)	0.003	0.30	27
Bacular mass (g) versus body length (cm)	<241 cm	+	SLR	7.34 (6.61, 8.07)	-16.2 (-17.9, -14.5)	<0.0001	0.91	44
Bacular mass (g) versus body length (cm)	>242 cm	=	SLR	1.94 (0.75, 3.12)	-3.21 (-6.12, -0.30)	0.002	0.31	27
Bacular density (g/cm) versus body length (cm)	<241 cm	+	SLR	5.24 (4.65, 5.84)	-12.4 (-13.8, -11.1)	<0.0001	0.88	44
Bacular density (g/cm) versus body length (cm)	>242 cm	=	SLR	1.53 (0.53, 2.52)	-3.46 (-5.91, -1.02)	0.004	0.27	27
Bacular mass (g) versus bacular length (cm)	All data	+	GMR/SLR	3.81/3.75 (3.68, 3.94)	-3.23/-3.17 (-3.38, -3.08)	<0.0001	0.97	103
Bacular mass (g) versus bacular length (cm)	<12.5 cm	+	GMR/SLR	3.44/3.27 (3.08, 3.80)	-2.86/-2.70 (-3.22, -2.50)	<0.0001	0.91	38
Bacular mass (g) versus bacular length (cm)	>12.9 cm	+	GMR/SLR	4.33/4.14 (4.01, 4.65)	-3.87/-3.64 (-4.26, -3.48)	<0.0001	0.92	65
Basal + shaft diameters (cm) versus bacular length (cm)	All data	+	GMR/SLR	1.38/1.34 (1.31, 1.46)	-0.858/-0.810 (-0.944, -0.772)	<0.0001	0.93	92
Basal + shaft diameters (cm) versus bacular length (cm)	<12.5 cm	+	GMR/SLR	1.23/1.07 (1.10, 1.45)	-0.718/-0.549 (-0.941, -0.496)	<0.0001	0.76	33
Basal + shaft diameters (cm) versus bacular length (cm)	>12.9 cm	+	GMR/SLR	1.69/1.52 (1.50, 1.88)	-1.23/-1.04 (-1.46, 0.99)	<0.0001	0.82	59
Apical diameters (cm) versus bacular length (cm)	<12.5 cm	=	GMR/SLR	1.19/0.751 (0.84, 1.53)	-1.11/-0.666 (-0.77, -1.45)	0.0001	0.40	32

TABLE 2.—Continued.

Log Y versus log X variable	Range of X variable	Allometry ^a	SLR or GMR	Slope (95% CI)	Intercept (95% CI)	P	R ²	N
Apical diameters (cm) versus bacular length (cm)	>12.9 cm	+	GMR/SLR	2.66/2.42 (2.36, 2.96)	-2.70/-2.41 (-3.06, -2.34)	<0.0001	0.82	59
Apical diameters (cm) versus basal + shaft diameters (cm)	<4.4 cm	=	GMR/SLR	1.00/0.706 (0.74, 1.26)	-0.432/-0.288 (-0.564, -0.300)	<0.0001	0.53	29
Apical diameters (cm) versus basal + shaft diameters (cm)	4.4 cm < X < 6.4 cm	+	GMR/SLR	2.64/2.33 (1.96, 3.32)	-1.53/-1.31 (-2.03, -1.03)	<0.0001	0.71	25
Apical diameters (cm) versus basal + shaft diameters (cm)	>6.4 cm	-	GMR/SLR	0.776/0.463 (0.559, 0.993)	0.065/0.214 (-0.108, 0.278)	0.0001	0.36	36

^a For Y relative to X: +, positive allometry; =, isometry; and -, negative allometry.

adulthood and adulthood (>10 years of age).

We distinguished only 2 phases of relative growth between bacular mass and length because we lacked specimens that adequately represented the 1st year of life. Slopes of allometric regression (SLR) for the 2 phases are strikingly similar between *Eumetopias* and *Odobenus*: 3.3 versus 3.2, and 4.1 versus 5.0, respectively. Therefore, it is apparent that substantial growth in mass (due to bacular thickening) in both species takes place late in life (beginning during sexual maturation in *Eumetopias*).

Positive allometry of mass:length also characterizes bacular growth in *A. p. pusillus* and *Callorhinus*. Estimates of GMR for bacular mass (Y) in relation to bacular length (X) are $Y = -2.89 + 3.49X$ and $Y = -2.77 + 3.35X$, respectively, for animals after their 1st year of life (adults in those samples had average standard lengths of 186 and 188 cm, respectively—W. H. Oosthuizen and E. H. Miller, in litt.; E. H. Miller, in litt.). *Eumetopias* had a lower intercept and steeper slope in our study ($Y = -3.23 + 3.81X$), in keeping with the high bacular density in adults of that species.

Apical growth also increased strikingly relative to bacular length beginning at 5–7 years of age. Concurrently, apical growth surpassed (was positively allometric to) bacular thickness; this phase of positive allometry was followed by one in which apical size stabilized, resulting in weak negative allometry of apical size to bacular thickness. As noted above, apical size and shape are more diverse and probably of more direct functional (stimulatory) significance in otariids than phocids. Apical anatomy and growth clearly merit more detailed attention in future studies.

In summary, the baculum of the Steller sea lion is much denser (relatively thicker) than in most otariids, and exhibits complex patterns of relative growth. Understanding the developmental basis of these patterns will require larger samples of animals ≥ 2 years of age plus larger samples and more

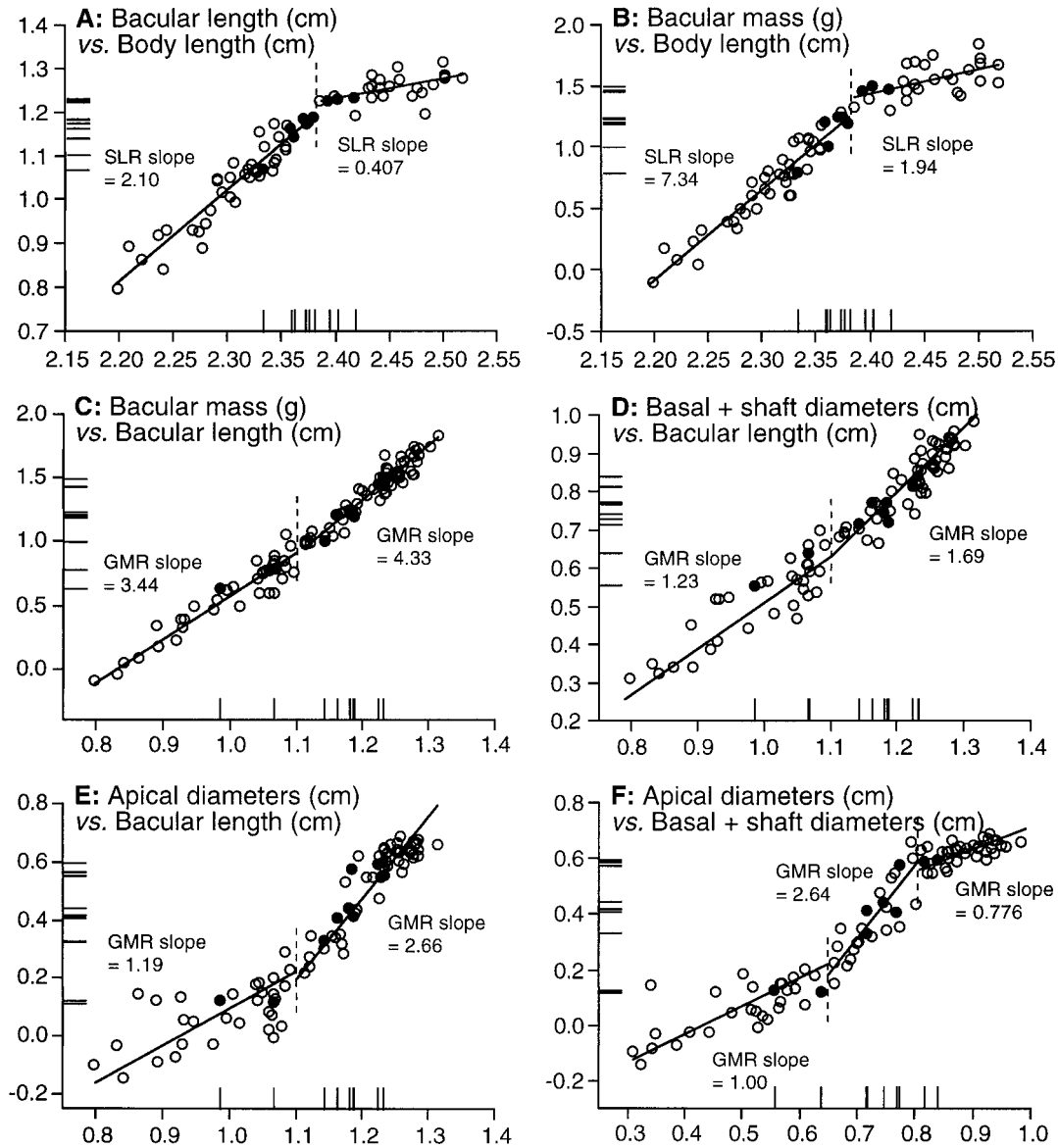


FIG. 2.—Allometric regression between selected variables. Regression lines and slopes from simple linear regression (SLR) or geometric mean regression (GMR) are shown as appropriate. Breaks between size ranges are shown as vertical dashed lines. Specimens aged 4.8–6.5 years (black circles; also shown as tick marks along each axis for clarity) span the breaks in all plots.

comprehensive information on individual specimens of animals 3–7 years of age (e.g., testicular size, assessment of spermatogenesis). Comparative investigations of bacular strength and structure are needed to assess the adaptive significance of bac-

ular thickness and density in terms of resistance to fracture.

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