

BACULAR AND TESTICULAR GROWTH, ALLOMETRY,
AND VARIATION IN THE HARP SEAL
(*PAGOPHILUS GROENLANDICUS*)

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We investigated quantitative relationships of bacular size to age, length of body, and testicular size in the harp seal (*Pagophilus groenlandicus*), based on collections made in the northwestern Atlantic from 1985 to 1992. Bacular growth was faster than growth in length of body except in old seals (>9 years of age), in which relative growth was isometric. A pubertal spurt in growth in bacular size occurred between 3 and 4 years of age when length increased by 48.3%, mass by 331%, and density by 185%. Concurrently, length of body showed a spurt in growth of 7.2%. Bacular length reached 90% of its asymptotic size of 17.4 cm at ca. 9 years of age, and bacular mass reached that point relative to its asymptote (49.6 g) later at ca. 20 years. In contrast, length of body reached 90% of asymptotic size (176 cm) at only 5–6 years of age. In old seals, bacular length was correlated positively with length of body and age independently. It averaged 9.9% of length of body in old seals. Bacular size was variable: $CV = 8.3\%$ for bacular length and 32.8% for bacular mass in old seals. Testicular size peaked in February and March. For young seals (≤ 9 years old), growth in bacular length was isometric, and growth in bacular mass was positively allometric relative to testicular length and mass. In contrast, testicular length and mass of breeding old seals were not correlated significantly with bacular size, length of body, or age. In breeding old seals, testes averaged 10.1 cm in length (range = 7.4–13.2 cm, $CV = 10.9\%$) and 128 g in mass (range = 60.6–204 g, $CV = 24.9\%$), and testicular length averaged 5.7% of length of body. Variation in bacular and testicular size suggests that males have variable reproductive strategies. Comparative analyses on phocid species with known mating systems are needed to test this interpretation.

Key words: *Pagophilus groenlandicus*, harp seal, baculum, allometry, sexual selection, growth

The baculum is valuable in mammalian systematics because bacular size, shape, and complexity vary greatly across species and sometimes vary geographically within species (Hill and Harrison, 1987; Patterson and Thaeler, 1982; Simson et al., 1993; Thomas et al., 1994). Such diversity in bacular anatomy presumably results from sexual selection, including internal selection within the female (Burt, 1960; Eberhard, 1985, 1996; Patterson and Thaeler, 1982).

A common result of evolution through sexual selection is incidental achievement of reproductive isolation between populations, which can lead to speciation (Sibley, 1957; West-Eberhard, 1983). Hence, understanding rates and processes of mammalian speciation is likely to be improved through knowledge of bacular variation on both intra- and interspecific levels.

Bacula of pinnipeds have received little attention from evolutionary biologists be-

cause bones are simple compared with bacula of many other mammalian taxa and differ relatively little across species (Chaine, 1926; Mohr, 1963; Morejohn, 1975; Pohl, 1911). The relative simplicity and uniformity of bacular anatomy in pinnipeds seem paradoxical in light of diverse mating systems of pinnipeds and intense reproductive competition among males in many species. With such breeding characteristics, divergence in bacular form among populations and species might be predicted. To investigate this paradox, we studied specimens and data from the pinniped family (Phocidae) with the greatest diversity of breeding systems.

Our objectives were to describe bacular, penile, and testicular anatomy, growth, and size relative to mating systems, and interpret these relationships in terms of reproductive strategies, differentiation of populations, and speciation. This paper presents analyses of bacular growth and allometry in harp seals (*Pagophilus groenlandicus*). The species was chosen because a large collection of bacula from seals of known age and accompanying measurements on size of body and testes were available. Our study provides a useful model for comparative studies and sheds light on the species' unknown mating system (Dixson, 1987).

METHODS

Data and specimens used in this study were from harp seals collected in Newfoundland or Labrador from 1985 to 1992. Most animals were shot by personnel of the Department of Fisheries and Oceans or commercial sealers; others were caught incidentally in fishing gear. Many measurements were taken on each specimen, but only standard length was used for this study (American Society of Mammalogists, 1967). Mass of body was not used because it is so variable due to seasonal and interannual fluctuations in blubber (Chabot et al., 1995).

Age was estimated by counting dentinal growth layers in the lower canine (Bowen et al., 1983). Age was estimated to the nearest 0.1 years, assuming a birth date of 1 March (data were lumped into age classes for some analy-

ses). To represent fully adult seals, a subsample of specimens >9 years of age was used in many analyses (Fig. 1).

Penes were frozen in the field and then thawed and boiled for ca. 1 h in the laboratory. After boiling, all flesh was removed by hand. Bacula were air-dried at room temperature for several weeks and measured (length to 1 mm; mass to 0.1 g). Testes and epididymides were removed in the field, trimmed of extraneous tissue, separated from one another, and placed in 10% formalin or frozen. Frozen specimens subsequently were placed in 10% formalin. After fixation, specimens were stored in 70% ethanol. In the laboratory, specimens were dried by squeezing gently in a paper towel. Length and width of testes were measured to the nearest 0.1 mm; masses of testes and epididymides were measured to the nearest 0.1 g. Bacula from 706 seals and testes plus epididymides from 1,323 seals were used in this study.

In our sample of seals, growth of the body continued throughout life. Nevertheless, growth was sufficiently slow in older animals to permit estimation of asymptotic size. This was done in two ways following McLaren (1993). First, a generalized von Bertalanffy function was fitted to data on length of body, using data on seals >1 year old, and with x_0 estimated as 0.56. This method yielded an estimated asymptote (L_∞) for length of body of 175.5 cm. Second, in species with accelerated growth at puberty (e. g., polygynous species), it is desirable to treat post- and prepubertal growth separately (McLaren, 1993). Acceleration in growth occurs in the harp seal at puberty, particularly in the baculum. Therefore the Gompertz equation (McLaren, 1993) was fitted to data on bacular size for seals >3 years old, i. e., after the first inflection point apparent in Fig. 1. For comparison with bacular growth, a Gompertz equation was also fitted to data on length of body for seals >3 years old. This provided an estimate of $L_\infty = 175.9$ cm.

Simple linear regression was used for analyses relating bacular size to age. Simple linear regression was also used in allometric analyses relating bacular size to length of body, although alternative approaches (e. g., reduced major axis regression) are preferable on theoretical grounds because length of body is measured with error (McLaren, 1993). Even so, most published analyses report allometric relationships in terms of simple linear regression, measurement error for

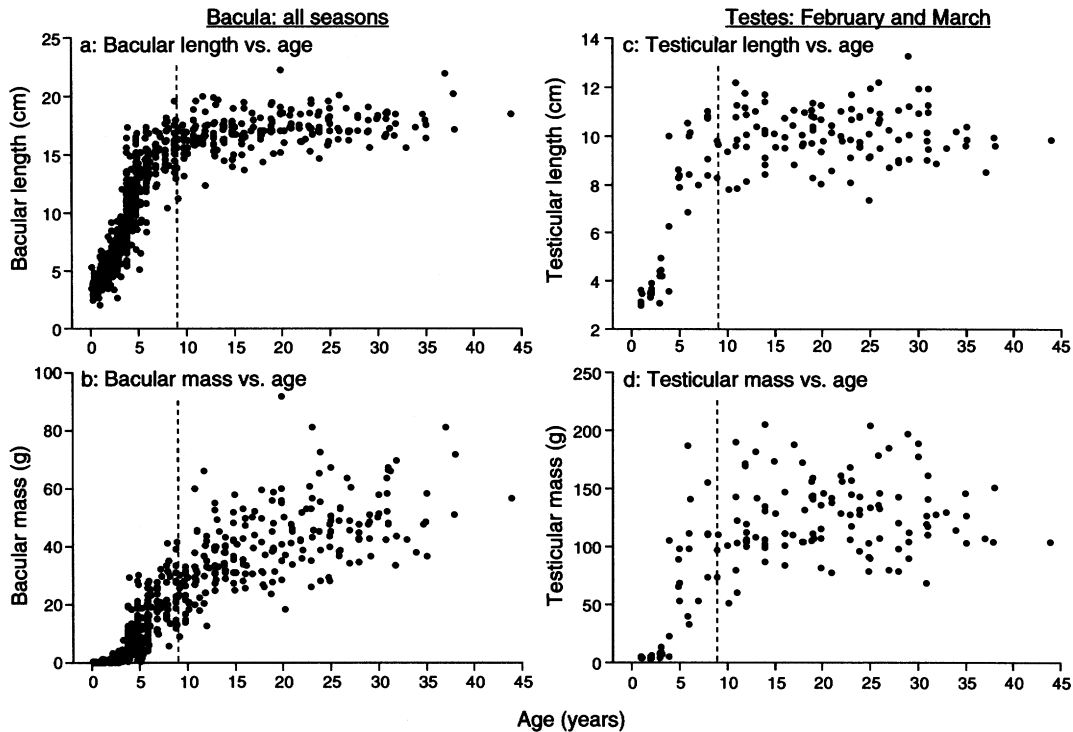


FIG. 1.—Growth in (a) bacular length, (b) mass for all specimens, (c) mean testicular length, and (d) mean mass for specimens collected in February and March. The vertical dashed lines separate old (>9 years of age) from young specimens.

this variable is small, and the correlation between bacular size and length of body is high (in reduced major axis regression, slope = b/r , where b is the slope from simple linear regression; thus estimates of slope are identical when $r = 1$ but differ substantially at low values of r). Therefore, we felt that simple linear regression was preferred (Dawson, 1994; Gould, 1966), but slopes from reduced major axis regression also were estimated where appropriate.

Seasonal variation in size of testes and epididymides was investigated for seals >9 years old. For those analyses, size was defined as the sum of lengths and widths of left plus right testes and as the sum of masses of left and right testes plus epididymides. Sums were used to reduce errors of individual measurements. Periodic (sine-cosine) regressions [$y_i = \beta_0 + \beta_1 \sin(x_i) + \beta_2 \cos(x_i) + e_i$] were fitted to these data from collections made throughout the year. In the regressions, dates corresponded to day of the year, with 0 = 1 January, 58 = 28 or 29 February, etc. The regressions were fitted to highlight trends in seasonal variation, not as a rig-

orous fit to the data. One-way analyses of variance across months for data on size of testes plus epididymides disclosed highly significant seasonal variation, with largest size in February and March (which formed a homogeneous subset in Student-Newman-Keuls multiple-range tests; Sokal and Rohlf, 1995). Specimens from February and March, therefore, were used to explore relationships of bacular size to size of body and testes plus epididymides.

General somatic growth and action of androgens must influence growth and size of the baculum in adult harp seals, as in other mammals (Williams-Ashman and Reddi, 1991). These relationships were investigated by including measurements of testes and epididymides in the analyses, as a proxy for androgenic effects. Analyses were restricted to seals collected in February and March, when testes and epididymides were largest (after March, spermatogenesis declines; Fisher, 1954).

Growth equations (von Bertalanffy and Gompertz), simple linear regression, reduced major axis regression, and periodic regressions were

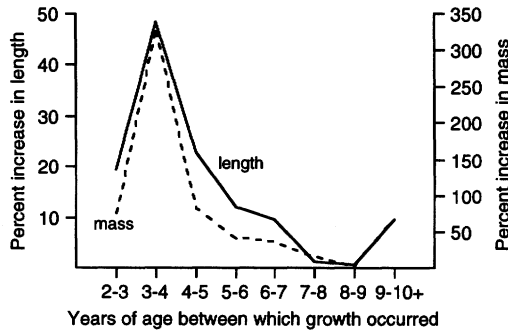


FIG. 2.—Incremental growth in bacular length and mass increased sharply at puberty (beginning at 3–4 years of age). The increase in incremental growth at 9–10+ years was an artifact, due to lumping of data on seals >9 years old.

fitted with Kaleidagraph 3.0 (Abelbeck Software, 2457 Perkiomen Avenue, Reading, PA). Analyses of variance were carried out with SuperAnova 1.11; other analyses were done with Statview 4.5 (Abacus Concepts, 1918 Bonita Avenue, Berkeley, CA).

RESULTS

The baculum exhibited sigmoidal growth in size (Fig. 1a, b). Asymptotic estimates were 17.4 cm for length, 49.6 g for mass, and 2.8 g/cm for density. The asymptotic estimate of bacular length as a percentage of length of body was 9.9%. Minimal and maximal values observed for seals >9 years old were 12.4 and 22.3 cm (length), 12.8 and 91.7 g (mass), and 0.96 and 4.2 g/cm (density).

Bacular growth was rapid in the period of presumed sexual maturation beginning at 3–4 years of age and continuing to 7 years of age (Figs. 1a, 1b, and 2). The most rapid growth was between 3–4 years when the baculum grew on average 48.3% in length, 331% in mass, and 185% in density (Fig. 2). Length of body also showed a minor spurt in growth (7.2%) between 3–4 years of age. Other evidence for the onset of puberty at 4 years of age came from allometric analyses of bacular and testicular size in young seals (≤ 9 years old) collected in February and March, in which 4-year-old specimens occupied a transitional position

(Fig. 3). Those specimens occupied a similar position in the relationship of testicular size to body length (Fig. 4).

Growth in bacular and body size slowed after sexual and physical maturity were attained (Fig. 1a and 1b) but continued throughout life (Table 1). Bacular growth slowed later in life than did growth in body size, as shown by asymptotic values. Age at which seals attained 90% of asymptotic length of body was 5–6 years. In contrast, 90% of growth in bacular length was reached at ca. 9 years of age, and bacular mass reached that point later at ca. 20 years (Fig. 5); 90% of growth in bacular density was reached at an intermediate age.

Variation in bacular size was high, especially among mature seals (Fig. 1a and 1b); the CV for 204 bacula from seals >9 years old was 8.3% in length, 32.8% in mass, and 27.6% in density. By comparison, the CV for length of body for the same sample of seals was 5.5%. Similar estimates of CV for length of body have been made for mature harp seals (4.6–4.9%; Hammill et al., 1995) and for several age classes of northern fur seals, *Callorhinus ursinus* (4.2–4.8%; Scheffer and Wilke, 1953).

When data on seals of all ages were considered, growth of the baculum was faster than growth in body size (Table 2), with slopes from log-log regression being several times higher than isometry. For seals >9 years old, bacular length increased slightly more slowly than length of body (slope <1), but bacular mass and density scaled isometrically (slopes of ca. 3 and ca. 2, respectively). Based on partial-correlation analysis, bacular length was correlated positively with length of body and age independently in seals >9 years old ($P < 0.001$ and 0.01, respectively). Bacular length increased isometrically with testicular size in specimens 3–9 years old from February and March, and bacular mass exhibited positive allometry (Fig. 3, Table 3). Testicular size increased sharply after length of body surpassed ca. 155 cm (Fig. 4).

For seals >9 years old in February and

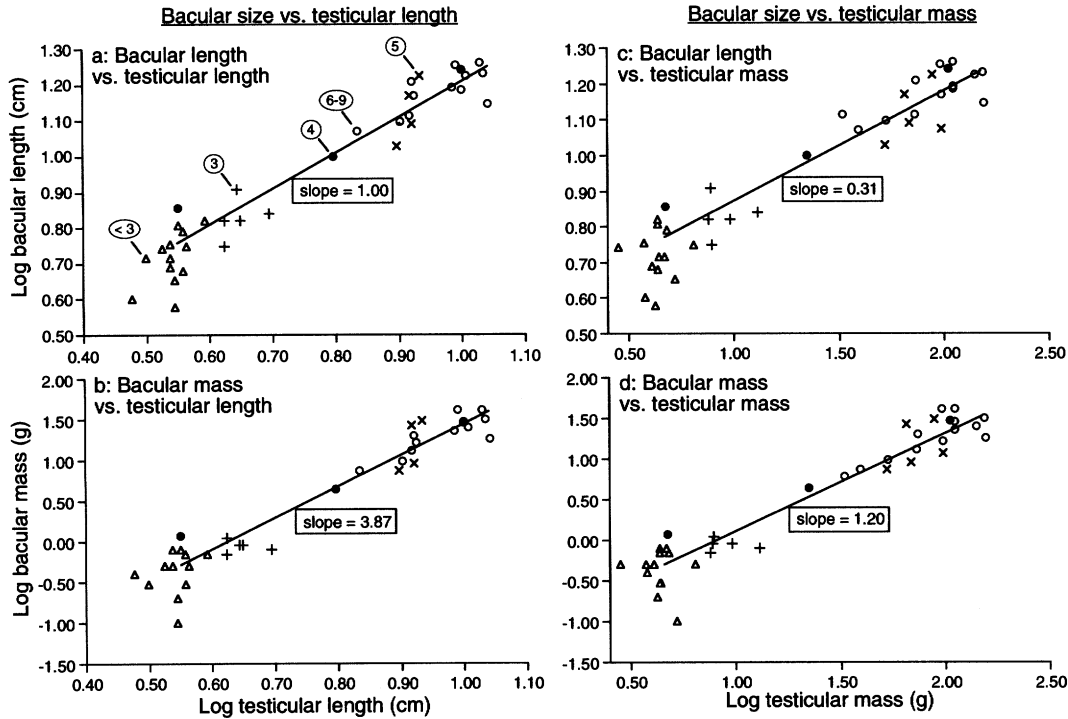


FIG. 3.—Scaling relationships of bacular size to mean testicular size for young seals (≤ 9 years old) collected in February and March. Age classes corresponding to different symbols are noted in (a). Note that the three 4-year-old specimens (solid circles) differed greatly in size, suggesting the onset of physiological sexual maturity at that age. Regression lines and slopes from simple linear regression are shown, for seals 3–9 years of age only (other results of regression analyses are in Table 3).

March, testes averaged 10.1 ± 1.11 (*SD*) cm in length ($n = 80$) and 128 ± 31.8 g in mass ($n = 84$; Fig. 1c and 1d). Length of testis averaged 5.7% of length of body for seals in that sample. Testes from those old seals varied greatly in size; length ranged from 7.4–13.2 cm ($CV = 10.9\%$) and mass ranged from 60.6–204 g ($CV = 24.9\%$). During the breeding period, testicular length and mass were independent of bacular length, bacular mass, length of body, and age ($P > 0.05$ for all estimates of r and partial- r ; Fig. 6).

DISCUSSION

Male harp seals in our sample grew quickly in length of body between 3–4 years of age. A spurt in growth has not been noted in previous studies (Innes et al., 1981;

Laws, 1959; McLaren, 1993; Sergeant, 1973a), perhaps because of its relative weakness. The spurt in somatic growth is concurrent with that in bacular size but is much weaker, so bacular growth is not merely a reflection of overall growth.

Sperm in testes and epididymides was noted in ca. 50% of males 4 years of age collected from the northwestern Atlantic in the late 1970s (I.-H. Ni, pers. comm.) and the White Sea in 1958 to 1964 (Yakovenko and Nazarenko, 1967); both studies, therefore, documented sexual maturation of males at near the maximal rate attainable by the species (Sergeant, 1973b). Our observations on incremental bacular growth agree with those findings, suggesting that it may be a good indicator of puberty in male seals. Increased bacular growth around pu-

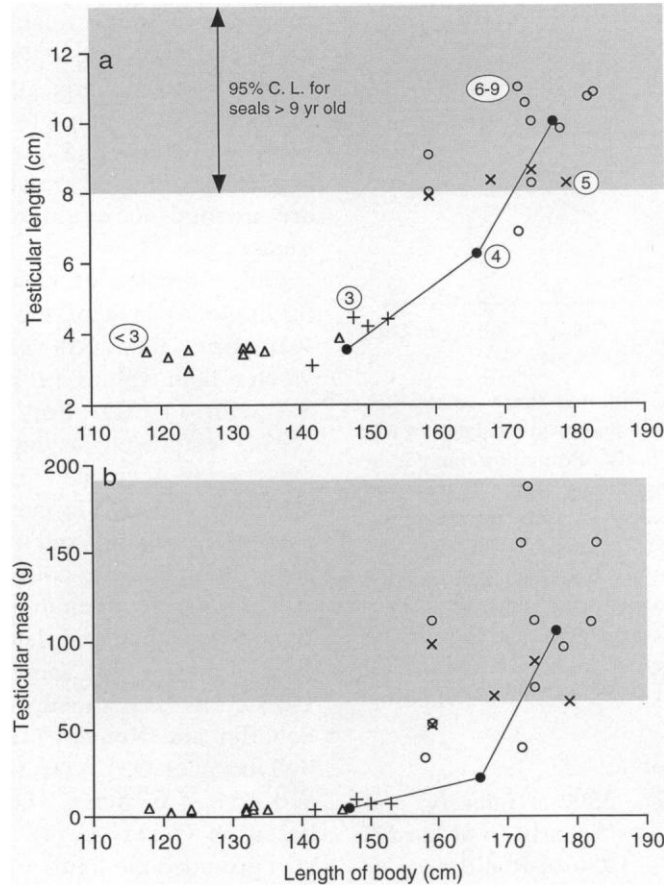


FIG. 4.—Relationships of mean testicular size to length of body for young seals (≤ 9 years old) collected in February and March. Age classes corresponding to different symbols are noted in (a). Note the sharp increase in testicular size for seals > 155 cm in length of body.

berty has been noted previously in harp seals and other phocids (Fisher, 1954; Hav- inga, 1933; McLaren, 1958a, 1958b; Ser- geant, 1991) but appears to have been men- tioned quantitatively only for the leopard seal (*Hydrurga leptonyx*). For that species, Hamilton (1939) noted differences of ca. 36% in bacular length and ca. 380% in bac-

ular mass between several 2- and 3-year-old specimens—strikingly similar to our values for the harp seal (48% and 331%, respec- tively). However, estimates of age at sexual maturity for male leopard seals are equiv- ocal (Laws, 1984). In contrast, bacular length in the highly polygynous southern elephant seal (*Mirounga leonina*) appears to

TABLE 1.—Summary of results from simple linear regression of bacular measurements and length of body on age (in years) for seals > 9 years old. All regressions were significant at $P < 0.001$.

Dependent variable	<i>n</i>	Intercept \pm SE	Slope \pm SE	r^2
Length of body (cm)	319	16.1 \pm 1.32	0.56 \pm 0.07	0.18
Bacular length (cm)	204	15.9 \pm 0.26	0.07 \pm 0.01	0.12
Bacular mass (g)	204	22.2 \pm 2.22	0.98 \pm 0.11	0.30
Bacular density (g/cm)	204	1.43 \pm 0.11	0.05 \pm 0.01	0.30

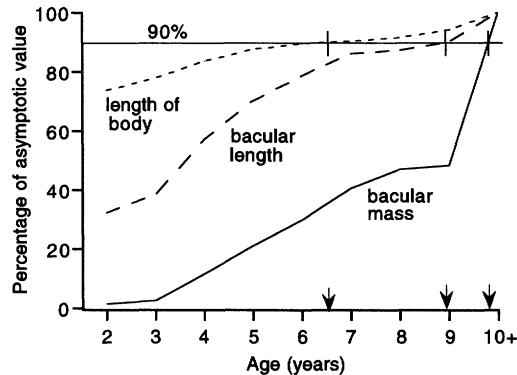


FIG. 5.—Bacular size of harp seals approached an asymptotic value much later in life than did length of body. Points on curves at which 90% of asymptotic growth was reached are marked by vertical lines, with corresponding points on the abscissa indicated by arrows. Asymptotic values were estimates from fitting the Gompertz equation. The sharp increase in bacular mass between 9–10+ years of age was an artifact, due to lumping of data on seals >9 years old; the actual value of the asymptote is ca. 20 years.

increase by only ca. 25% at puberty, and bacular density grows linearly to at least 9 years of age (Laws, 1956a). Rapid bacular growth may characterize “more precocious” phocid species (Laws, 1956a:5), but bacular length in *M. leonina* only reaches

about one-half the relative size of that in harp and leopard seals (Dixson, 1995; Scheffer and Kenyon, 1963). Quantitative estimates of bacular growth at puberty in other pinnipeds and their relationship to concurrent rates of growth in size of body are needed to evaluate properly these trends.

Our estimates of absolute and relative (asymptotic) size of the baculum in harp seals from the northwestern Atlantic are greater than values in Fisher (1954) and Sergeant (1991). For example, Fisher (1954) estimated asymptotic length and mass as 16.4 cm and 33.9 g (maxima = 19.8 cm and 67.8 g, respectively), compared with 17.4 cm and 49.6 g in this study. Their samples were collected from 1949 to 1957, however, when harp seals were likely smaller and matured later (Bowen et al., 1981; Laws, 1959; Sergeant, 1966, 1973a, 1973b, 1991). Estimates of bacular size by Scheffer and Kenyon (1963:39), and used by Dixson (1995), were 185+ mm in length and 66+ g in mass. The latter value was based on Fisher (1954), who ambiguously also provided the figure of 67.8 g. Estimates of length of body used by Scheffer and Kenyon (1963) were taken from Sivertsen’s (1941) data on harp seals from the White

TABLE 2.—Summary of results from simple linear regression of \log_{10} (bacular measurements) on \log_{10} (length of body). Bacular growth was positively allometric relative to length of body for all ages combined (first three rows). For seals >9 years old¹, bacular length showed slightly negative allometry, but bacular mass and density grew isometrically.²

Dependent variable	Age	n	Slope (95% CI) ³	Expected slope for isometry	Intercept (95% CI)	r ²
Bacular length (cm)	All	539	3.84 ⁴ (3.34, 3.62)	1	−6.58 (−6.89, −6.27)	0.81
Bacular mass (g)	All	542	12.8 ⁴ (12.3, 13.3)	3	−27.2 (−28.2, −26.1)	0.84
Bacular density (g/cm)	All	539	9.30 ⁴ (8.93, 9.65)	2	−20.5 (−21.3, −19.7)	0.82
Bacular length (cm)	>9 yr	162	0.65 (0.43, 0.88)	1	−0.23 (−0.73, 0.27)	0.18
Bacular mass (g)	>9 yr	162	3.08 (2.21, 3.96)	3	−5.31 (−7.26, −3.35)	0.24
Bacular density (g/cm)	>9 yr	162	2.43 (1.69, 3.17)	2	−5.08 (−6.74, −3.42)	0.21

¹ Only specimens >9 years old with length of body >155 cm were used because this value is close to when sexual maturity seems to be achieved (Fig. 4).

² $P < 0.001$ for all regressions.

³ Slopes in reduced major axis regression were 3.86, 14.0, 10.2, 1.48, 6.10, and 5.12, respectively.

⁴ Slopes (and 95% CI) based on simple linear regression using means for all age classes ($n = 11$, for age classes 0, 1, . . . , 9, >9) were: bacular length, 4.14 (3.78–4.50); bacular mass, 14.0 (12.3–15.6); and bacular density, 9.73 (8.37–11.1), respectively. Corresponding slopes in reduced major axis regression were 4.17, 14.1, and 9.90, respectively.

TABLE 3.—Summary of results from simple linear regression of \log_{10} (bacular measurements) on \log_{10} (mean testicular measurements) for young seals (3–9 years old) in February and March. Relative growth in bacular length was isometric relative to testicular size; that in bacular mass was positively allometric.¹

Dependent variable	Independent variable	n	Slope (95% CI) ²	Expected slope for isometry	Intercept (95% CI)	r ²
Bacular length (cm)	Testicular length (cm)	24	1.00 (0.84, 1.16)	1	0.21 (0.08, 0.35)	0.8
Bacular length (cm)	Testicular mass (g)	24	0.31 (0.26, 0.36)	0.33	0.57 (0.48, 0.66)	0.8
Bacular mass (g)	Testicular length (cm)	26	3.87 (3.34, 4.40)	3	-2.43 (-2.90, -1.96)	0.9
Bacular mass (g)	Testicular mass (g)	26	1.20 (1.04, 1.37)	1	-1.07 (-1.36, -0.79)	0.9

¹ P < 0.001 for all regressions.

² Slopes in reduced major axis regression were 1.06, 0.33, 4.05, and 1.26, respectively.

Sea. In his study, Sivertsen (1941) measured length of body from the tip of the nose to the end of the rear flippers, yielding greater values than for standard length. Given the mixed and approximate nature of measurements available to Scheffer and Kenyon (1963), and geographic and temporal variation in body size, it is remarkable that their estimate of the ratio of length of baculum to length of body in adults (10.8%) differs little from ours (9.9%).

Testicular size in mammals is affected by length of the breeding period and mating competition (Kenagy and Trombulak, 1986), so it is important to obtain good es-

timates of testicular size for comparative analyses. Available information on the harp seal is variable. We estimated testicular mass of mature males in February and March as 128 g per testis. This value cannot be readily compared with other published estimates for the species, partly because they include measurements from outside the period of maximal testicular size. In their study in the White Sea, for example, Yakovenko and Nazarenko (1967) estimated testicular mass (presumably testes combined) of 5- and 6-year-old harp seals collected in March and April as 158 and 165 g. In our study, a comparable subsample

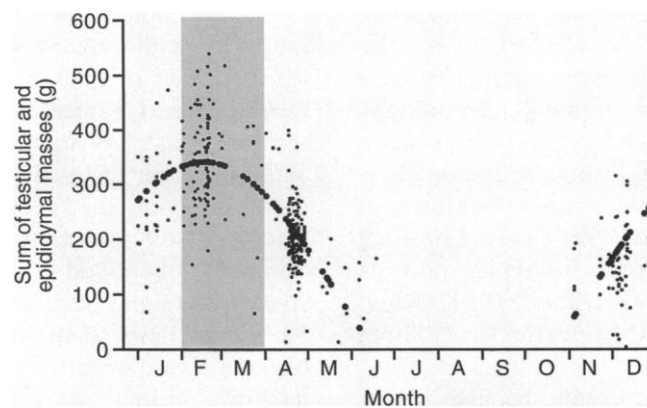


FIG. 6.—Size of testis and epididymis of harp seals varied seasonally; largest size occurred in February and March. The sum of masses of left and right testes plus epididymides are plotted for males >9 years old; linear measurements show an identical trend. Data used for partial-correlation analyses are in the shaded section, which covered the breeding period; a datum with the smallest value was excluded from all analyses. The curve was fitted by sine-cosine regression to highlight trends in seasonal variation.

has a mean mass (both testes) of 111 g. Five 10-year-old seals collected in the same months in the northwestern Atlantic in 1952-1957 averaged 158 g in testicular mass (presumably both testes combined; Sergeant, 1991), compared with an estimate from our study of 135 g (both testes). Lastly, collections made in 1971 (unspecified months) averaged ca. 195 g for 6-year-olds and 175 g for 10-year-olds (presumably both testes combined; Sergeant, 1973*b*). Testicular specimens from the Barents Sea collected throughout the year are ca. 25% heavier than in our sample (Kjellqwist et al., 1995). Differences in reporting and techniques of cleaning, preservation, and measurement of specimens clearly need to be minimized in future studies, for data to be useful in comparative analyses.

Intraspecific allometry can be characterized in several ways. Growth-related allometry can be based on longitudinal studies of individuals or by using samples of different age classes. Intraspecific studies also can investigate allometry within samples of similarly aged animals (usually adults). Analyses of the latter two types are presented in this paper. They indicate strong positive allometry of bacular size relative to size overall, but beginning at ca. 10 years of age, isometry in bacular mass and weak negative allometry or isometry in bacular length occur, with growth continuing at a low rate. For mature animals, this finding is in agreement with the general observation that skeletal growth in mature pinnipeds is roughly isometric with other measures of body size (Bryden, 1969, 1972). Life-long bacular growth appears to typify phocids and other Carnivora (Elder, 1951; King, 1991; Powell, 1982; Scheffer and Slipp, 1944).

Among older harp seals, bacular size is affected independently by both age and size of body (the interrelationships of these factors are well shown by 4-year-old seals; Fig. 4). These relationships may reflect a common response of somatic and reproductive growth to androgens; some individuals

may be large for their age and have large genitals because of unusually high levels of androgens (or have unusually high levels of androgens at puberty, with later growth being a carry-over). High variation in absolute and relative bacular size among individuals of the same age is common (Arata et al., 1965; Bester, 1990; Elder, 1951; Long and Frank, 1968; Scheffer, 1950). Such high intraspecific variation probably is related to variation in age at sexual maturity, which in turn is linked to variation in somatic growth commonly affected by ecological factors (Arata et al., 1965; Bryden, 1968; Chabot et al., 1995; Hammill et al., 1995; Laws, 1956*b*, 1959, 1984).

Whatever the proximate cause, size of genitals is known to differ among species of animals with different mating systems and levels of reproductive competition (Dahl et al., 1993; Dixon, 1987; Harcourt et al., 1981; Kenagy and Trombulak, 1986; Møller, 1988; Short, 1979). Such relationships have not been investigated systematically for pinnipeds either within or across species, although scattered observations suggest that intraspecific differences in androgenic levels, size of body, and size of genitals within species are reflected in social behavior and status. Thus, Scheffer (1950:389) noted that northern fur seals (*C. ursinus*) "with longer bodies and larger testes haul out on land earlier than do their fellows," and Roberts (1988) found that territorial males of that species were larger and had larger testes than did nonbreeding individuals of the same age. Similarly, Thorsteinson and Lensink (1962) mentioned the likelihood that their estimates for size of body and baculum in young mature Steller sea lions (*Eumetopias jubatus*) were biased upward because the sample included territorial animals only and excluded non-territorial ones of the same age.

To understand relationships of bacular growth and size to reproductive competition in pinnipeds, data are needed on penile anatomy, bacular and penile function in intromission and copulation, and size and

conformation of the female reproductive tract (Brown et al., 1995; Dahl et al., 1993). These functions likely differ among species (Dixon, 1995; Hill and Harrison, 1987; Le Boeuf, 1972; Miller et al., 1996; Patterson, 1983). In phocids, for example, the baculum does not protrude beyond the glans penis, but it does in otariids (Green, 1972; Harrison, 1969; Harrison et al., 1952; Tedman, 1991). Laws and Sinha (1993:234) note that in *A. gazella* "the glans . . . forms a hollow collar of erectile tissue, in the centre of which the baculum forms a conical prominence." Such an arrangement suggests a fairly direct role of the baculum in stimulating the female reproductive tract; if it typifies otariids, it may explain why the otariid baculum is more morphologically diverse than the phocid baculum (Mohr, 1963; Morejohn, 1975). Endocrinological influences on growth (somatic and reproductive) at puberty and later in life need to be investigated because these likely account for much of the bacular variation within species (Arata et al., 1965). Bacular development needs to be described because it is complex and differs among species (Arata et al., 1965; Evans, 1993; Vilmann, 1982). Quantitative relationships of bacular and genitalic size to size of body in specimens of known age need to be investigated for other species of seal throughout development and for breeding adult males.

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