CHAPTER 5

Age determination and growth in the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): part three, baculum

C. L. Stewardson and T. Prvan

Manuscript submitted 2001.

ABSTRACT

Morphology, relative size and growth of the baculum in 103 Cape fur seals, *Arctocephalus pusillus pusillus*, from the Eastern Cape coast of South Africa are described. Bacular measurements (n = 8 linear variables and mass) were examined in relation to standard body length (SBL), bacular length and chronological age (y) using linear regression. Animals ranged from < 1 mo to ≥ 12 y. Bacular shape was most similar to *Callorhinus* and *Zalophus*. For the range of ages represented in this study, the baculum continued to increase in size until at least 10 y, with growth slowing between 8–10 y, when social maturity (full reproductive capacity) is attained. Growth in bacular length, distal height and bacular mass peaked at 8 y; middle shaft height and distal shaft height peaked at 9 y; proximal height, proximal width, distal width and proximal shaft height peaked at 10 y. In the largest animals (age unknown), maximum bacular length was 139.3 mm and mass 12.5 g. Relative to SBL, bacular length increased rapidly in young animals, peaked at 9 y (6.9%), and then declined. Bacular mass and distal height expressed greatest overall growth, followed by proximal height, proximal shaft height and bacular length. At 9 y, mean bacular length and mass was 117 mm and 7 g; growth rates in bacular length and mass were 311% and 7125% (relative to age zero), and 5% and 27% (between years); and bacular length averaged 6.9% of SBL. For all males ≥ 12 mo, most bacular variables grew at a faster rate than SBL and bacular length. Exceptions included proximal width which was isometric to SBL; distal width and distal shaft height which were isometric to bacular length; and proximal width which was negatively allometric relative to bacular length. Bacular length was found to be a 'rough indicator' of SBL and seal age group (pup, yearling, subadult, adult), but not of absolute age.

Key words: Pinnipeds, baculum, growth, allometry

INTRODUCTION

The mammalian baculum (os penis) is found in all carnivores, except the hyena (Ewer, 1973). This morphologically diverse bone has received considerable scientific attention in the field of mammalian systematics (McLaren, 1960; Sutton & Nadler, 1974; Kim *et al.*, 1975; Morejohn, 1975; Lee & Schmidly, 1977; Patterson & Thaeler, 1982; Patterson, 1983), and has been used as an index of age, puberty and social maturity for several species of mammals, including pinnipeds (Hamilton, 1939; Elder, 1951; Laws, 1956; Hewer, 1964; Bester, 1990). The function of the mammalian baculum remains controversial. It may lack specific function (Burt, 1939; Mayr, 1963) or may be adaptive in various interactions of males and females during copulation, with function differing considerably between species (Scheffer & Kenyon, 1963; Long & Frank, 1968; Ewer, 1973; Miller, 1974; Morejohn, 1975; Patterson & Thaeler, 1982; Eberhard, 1985, 1996; Dixson, 1995; Miller *et al.*, 1996, 1998, 1999).

Within the Otariidae, information on the morphology of the baculum is available for *Arctocephalus pusillus*, Afro-Australian fur seal; *Arctocephalus gazella*, Antarctic fur seal; *Callorhinus ursinus*, northern fur seal; *Eumetopias jubatus*, northern (Steller) sea lion; *Neophoca cinerea*, Australian sea lion; *Otaria byronia*, South American fur seal; *Phocarctos hookeri*, New Zealand (Hooker's) sea lion; and *Zalophus californianus*, California sea lion (Chaine, 1925; Hamilton, 1939; Rand, 1949, 1956; Scheffer, 1950; Mohr, 1963; Scheffer & Kenyon, 1963; Kim *et al.*, 1975; Morejohn, 1975; Laws & Sinha, 1993). Of these, the northern fur seal has been studied in most detail (Scheffer, 1950; Scheffer & Kenyon, 1963; Kim *et al.*, 1975; Morejohn, 1975).

Information on bacular growth based on animals aged from tooth structure, or on animals of known-age (i.e., animals tagged or branded as pups), is only available for the northern fur seal (Scheffer, 1950); *Arctocephalus tropicalis*, subantarctic fur seal (Bester, 1990); and *Arctocephalus pusillus pusillus*, Cape fur seal (Oosthuizen & Miller, 2000). These studies indicate that: (i) the baculum increases in length and mass with increasing age; (ii) bacular growth may be fairly constant, as in the northern fur seal and subantarctic fur seal, or there may be an increase in the rate of growth at puberty, as in the Cape fur seal; (iii) there may be a sudden increase in the rate of bacular growth when individuals attain social maturity (full reproductive capacity); and (iv) there is a decline in the rate of bacular growth in socially mature animals.

Here we examine the bacula of 103 male Cape fur seals from the Eastern Cape coast of South Africa. Specific objectives were to: (i) describe the general morphology of the baculum; (ii) quantify growth of bacular measurements (n = 8 linear variables and mass) relative to standard body length (n = 89 animals), bacular length (n = 100 animals), and chronological age (n = 50 animals); (iii) determine if the baculum is a useful indicator of social maturity; and (iv) determine if bacular length is a useful indicator of age and/or standard body length. This study is the third in a series of papers initiated to develop baseline descriptions of Cape fur seal morphology and to examine growth patterns.

MATERIALS AND METHODS

Collection of specimens

Cape fur seals were collected along the Eastern Cape coast of South Africa between Plettenberg Bay (34˚ 03'S, 23˚ 24'E) and East London (33˚ 03'S, 27˚ 54'E), from August 1978 to December 1995, and accessioned at the Port Elizabeth Museum (PEM). From this collection, bacula from 103 males were selected for examination (Appendix 5.1). Apart from specimens collected before May 1992 (n = 29), all specimens were collected by the first author. One animal (PEM2238) was collected NE of the study area, at Durban.

Preparation and measurement of bacula

Bacula were defleshed and macerated in water for 1–2 mo. Water was changed regularly. Bacula were then washed in mild detergent and air dried at room temperature. Dry specimens were weighed using an electronic balance and measurements (n = 8 linear variables) were taken using a vernier calliper (to 0.1 g and 0.1 mm) following Morejohn (1975) (Fig. 5.1). All bacular measurements, were recorded by the first author.

Age determination

Of the 103 animals in the study: (i) 40 were aged from counts of incremental lines observed in the dentine of upper canines as described in Stewardson *et al.*, (200X*a*). i.e., range 1–10 y; (ii) 10 were identified as adults > 12 y[1] (i.e., pulp cavity of the upper canine closed); and (iii) 52 were not aged.

For this study, the following age groups were used: pup (< 1 mo to 6 mo); yearling (7 mo to 1 y 6 mo); subadult (1 y 7 mo to 7 y 6 mo); and adult (≥ 7 y 7 mo) (Table 5.1). The following ages were not represented: 2 y and 3 y. Very old animals of known-age were not available for examination (estimated longevity *c.* 20 y).

Currently, examination of tooth structure is the most precise method of age determination in pinnipeds; however, counts are not without error. For information of the reliability of this method see Oosthuizen (1997).

Statistical analysis

Bacular measurement error

Duplicate measurements of bacular length were taken from 50 randomly selected bacula to assess measurement error. The Wilcoxon sign-rank test was

[1] In Cape fur seals, animals > 13 y can not be aged from counts of growth layer groups in the dentine of upper canines because the pulp cavity closes which terminates tooth growth, hence the age group '> 12 y'.

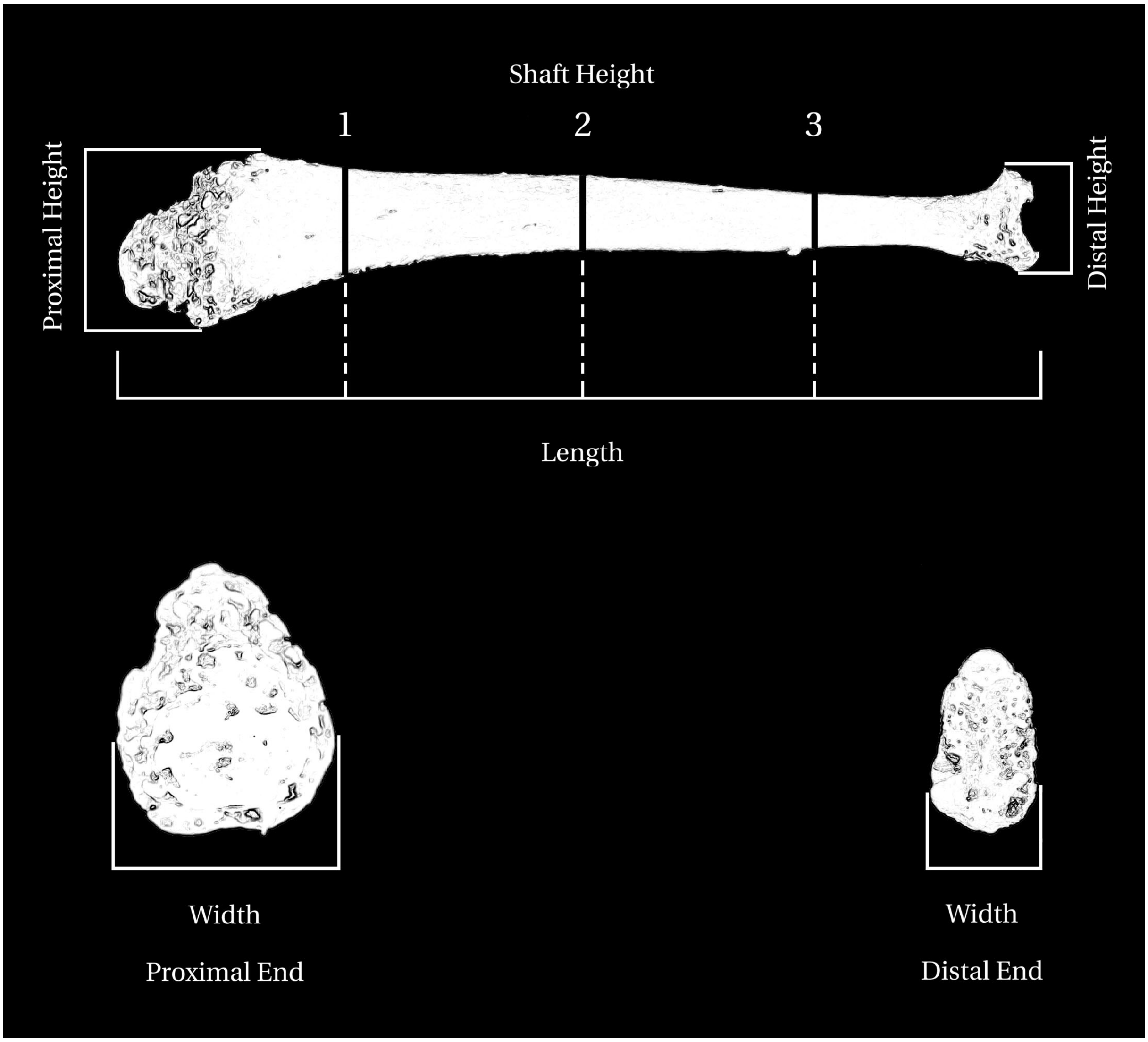

Fig. 5.1 Diagram of a Cape fur seal baculum showing how individual measurements were taken.
a. bacular length; b. proximal height; c. proximal width; d. distal height; e. distal width; f (1). proximal shaft height; f (2). middle shaft height; f (3). distal shaft height; g. bacular mass (not shown). Specimen provided by P. Shaughnessy.

used on the differences to test H_0 : median = 0, versus H_1 : median ≠ 0.

Bacular length expressed in relation to standard body length

Growth in bacular length, relative to standard body length (SBL), was calculated as follows, using paired samples only:

$$\text{bacular length (mm)}/\text{SBL (mm)} \times 100\%$$

As the approximate variance of the ratio estimate is difficult to calculate, percentages must be interpreted with caution (Cochran, 1977, p. 153).

Bacular growth relative to age zero, RGR $\bar{y}_0$

Percent change in bacular measurement at age *t*, relative to value at age zero, was calculated as follows:

$$[(\bar{y}_t - \bar{y}_0)/\bar{y}_0] \times 100\%$$

where $\bar{y}_0$ = bacular measurement from pups < 1 mo of age (age zero), and $\bar{y}_t$ = bacular measurement for age *t* (age class in y).

Bacular growth relative to the previous year, RGR $\bar{y}_{t-1}$

The percent change in value at age *t*, relative to the value at age *t*–1, was calculated as follows:

$$[(\bar{y}_t - \bar{y}_{t-1})/\bar{y}_{t-1}] \times 100\%$$

where $\bar{y}_t$ = as above, and $\bar{y}_{t-1}$ = bacular measurement for age *t*–1 (between years). RGRs were calculated for animals 7–10 y.

Bacular length as an indicator of SBL and age

The degree of linear relationship between log bacular length, log SBL and age (y) was calculated using the

Spearman rank-order correlation coefficient. Linear discriminant function analysis (Mahalanobis squared distance) was used to predict the likelihood that an individual seal will belong to a particular age group (pup, yearling, subadult, adult) using one independent variable, bacular length (see Stewardson *et al.*, 200X*a* for further details).

Bivariate allometric regression

The relationship between value of bacular measurement and: (i) SBL, (ii) bacular length, and (iii) age (y), was investigated using the logarithmic (base e) transformation of the allometric equation, $y = ax^b$, which may equivalently be written as $\log y = \log a + b \log x$. 'Robust' regression (Huber M-Regression) was used to fit straight lines to the transformed data. The degree of linear relationship between the transformed variables was calculated using the Spearman rank-order correlation coefficient, *r* (Gibbons & Chakraborti, 1992). Testing of model assumptions, and hypotheses about the slope of the line, followed methods described by Stewardson *et al.*, 200X*a*.

Statistical analysis and graphics were implemented in Minitab (Minitab Inc., State College, 1999, 12.23); Microsoft ® Excel 97 (Microsoft Corp., Seattle, 1997) and S-PLUS (MathSoft, Inc., Seattle, 1999, 5.1).

RESULTS

Bacular measurement error

Of the 50 bacula that were measured twice, measurements were reproducible at the 5% significance level (*p*-value = 0.03).

Table 5.1 ***The age distribution of Cape fur seals***

Age group	Age[a] (y)	Frequency	Percentage
Pup[b]	0	3	6.0
Yearling	1	5	10.0
Subadult	2	0	0.0
	3	0	0.0
	4	1	2.0
	5	3	6.0
	6	2	4.0
	7	11	22.0
Adult	8	8	16.0
	9	4	8.0
	10	3	6.0
	> 12	10	20.0
Total		**50**	**100**

[a] Age inferred from counts of incremental lines observed in the dentine of upper canine ($n = 40$). An additional 10 males were > 12 y, i.e., pulp cavity closed.
[b] < one month of age.

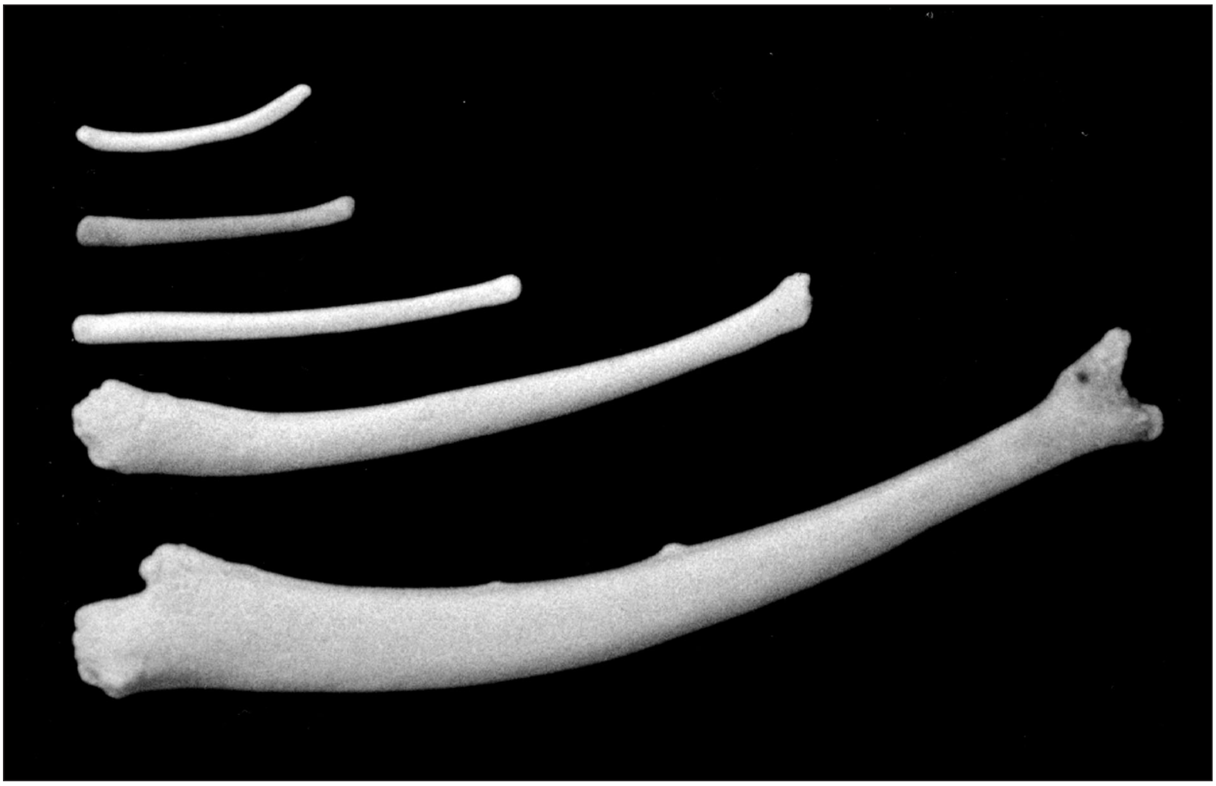

Fig. 5.2 Size and shape of the Cape fur seal baculum in relation to age group.
1. pup (PEM2020, 26.6 mm); 2. pup (PEM2024, 31.6 mm); 3. yearling (PEM2191, 50.7 mm); 4. subadult, 7-y-old (PEM2053, 93.3 mm); 5. adult, 10-y-old (PEM2087, 123.3 mm).

Table 5.2 ***Summary statistics for bacular variables (1–9), according to age (y) and age group.*** **Data presented as mean measurement ± S.E., followed by coefficient of variation in round brackets, and bacular variable expressed as a percentage of bacular length. Maximum value of each variable (males of unknown-age) is also presented. All measurements are in mm, apart from bacular mass (g).**

Age group	Age (y)	n[a]	Var 1	Var 2	Var 3	Var 4	Var 5	Var 6	Var 7	Var 8	Var 9
Pup	< 1	3	28.5 ± 1.6	2.6 ± 0.5	3.5 ± 0.3	2.2 ± 0.3	1.7 ± 0.2	2.4 ± 0.2	2.2 ± 0.2	1.9 ± 0.1	0.1 ± 0.0
			(9.6) –	(31.5) 9.0%	(12.5) 12.3%	(24.7) 7.8%	(18.3) 5.9%	(13.6) 8.3%	(15.7) 7.7%	(7.9) 6.8%	(0) 0.4%
Yearling	1	5	47.8 ± 1.7	3.5 ± 0.1	4.2 ± 0.1	2.9 ± 0.2	1.7 ± 0.04	3.0 ± 0.1	2.5 ± 0.1	2.2 ± 0.2	0.3 ± 0.03
			(8.0) –	(7.7) 7.3%	(6.6) 8.8%	(15.8) 6.1%	(5.9) 3.6%	(5.0) 6.2%	(12.2) 5.2%	(18.2) 4.6%	(23.6) 0.6%
Subadult	4	1*	86.6	5.3	6.6	7.3	2.8	5.9	5.5	4.4	2.4
	5	3	97.1 ± 4.6	9.4 ± 2.5	7.7 ± 0.9	9.4 ± 0.6	4.2 ± 0.8	7.0 ± 0.6	5.8 ± 0.2	5.0 ± 0.2	3.4 ± 0.4
			(8.2) –	(45.3) 9.7%	(20.9) 7.9%	(10.5) 9.7%	(31.0) 4.3%	(13.6) 7.2%	(4.6) 6.0%	(8.4) 5.1%	(21.2) 3.5%
	6	2	99.5 ± 2.8	8.2 ± 0.1	6.7 ± 1.5	10.9 ± 0.1	3.9 ± 0.6	7.1 ± 0.9	5.4 ± 0.2	4.5 ± 0.1	3.1 ± 0.1
			(3.9) –	(0.9) 8.2%	(31.7) 6.7%	(0.7) 10.9%	(20.2) 3.9%	(17.9) 7.1%	(5.2) 5.4%	(3.1) 4.5%	(2.3) 3.1%
	7	11	101.4 ± 2.7	9.8 ± 1.0	7.6 ± 0.4	10.7 ± 0.6	4.0 ± 0.2	7.2 ± 0.3	6.3 ± 0.3	5.3 ± 0.2	4.1 ± 0.4
			(9.0) –	(33.4) 9.7%	(16.3) 7.5%	(17.8) 10.5%	(17.5) 4.0%	(14.8) 7.1%	(13.3) 6.2%	(14.3) 5.3%	(34.0) 4.0%
	4–7	**17**	**99.5 ± 2.1**	**9.3 ± 0.8**	**7.5 ± 0.3**	**10.3 ± 0.4**	**4.0 ± 0.2**	**7.1 ± 0.2**	**6.1 ± 0.2**	**5.1 ± 0.2**	**3.7 ± 0.3**
			(8.7) –	(34.6) 9.3%	(17.5) 7.5%	(17.5) 10.3%	(20.5) 4.0%	(14.4) 7.1%	(12.5) 6.1%	(13.9) 5.1%	(33.1) 3.7
Adult	8	8	111.4 ± 3.1	11.3 ± 0.8	9.4 ± 0.6	12.2 ± 0.5	4.3 ± 0.1	8.0 ± 0.3	6.9 ± 0.2	5.6 ± 0.2	5.7 ± 0.5
			(7.8) –	(19.0) 10.8%	(18.5) 8.4%	(12.3) 11.0%	(9.5) 3.9%	(11.1) 7.2%	(8.7) 6.1%	(8.4) 5.0%	(23.9) 5.1%
	9	4	116.9 ± 2.7	10.4 ± 1.8	10.8 ± 1.6	12.4 ± 0.9	4.9 ± 0.7	8.1 ± 0.5	7.6 ± 0.3	6.3 ± 0.2	7.2 ± 0.7
			(4.6) –	(35.5) 8.9%	(29.3) 9.2%	(14.5) 10.6%	(29.2) 4.2%	(12.8) 7.0%	(7.9) 6.5%	(7.8) 5.4%	(18.4) 6.2%
	10	3	117.8 ± 2.9	14.0 ± 0.8	13.5 ± 1.9	13.2 ± 0.5	6.1 ± 0.4	10.6 ± 0.3	8.1 ± 0.4	6.5 ± 0.2	7.6 ± 0.6
			(4.3) –	(9.7) 11.9%	(24.5) 11.4%	(6.2) 11.2%	(12.5) 5.2%	(4.8) 9.0%	(8.1) 6.9%	(4.7) 5.5%	(14.1) 6.5%
	8–10	**15**	**114.2 ± 2.0**	**11.6 ± 0.7**	**10.6 ± 0.7**	**12.5 ± 0.4**	**4.8 ± 0.3**	**8.6 ± 0.3**	**7.3 ± 0.2**	**6.0 ± 0.1**	**6.5 ± 0.4**
			(6.6) –	(23.1) 10.2%	(26.4) 9.3%	(11.5) 10.9%	(22.0) 4.2%	(15.4) 7.5%	(10.6) 6.4%	(9.6) 5.2%	(23.2) 6.7%
	> 12	10	113.1 ± 3.8	11.4 ± 0.8	10.1 ± 0.7	13.3 ± 0.7	4.9 ± 0.5	10.0 ± 0.5 [8]	8.6 ± 0.6	6.6 ± 0.3	8.3 ± 0.9
			(10.7) –	(22.6) 10.1%	(20.9) 8.9%	(17.3) 11.7%	(28.4) 4.5%	(17.2) 8.8%	(23.6) 7.6%	(12.5) 5.8%	(34.2) 7.3%
Total		**50**	**50**	**50**	**50**	**50**	**50**	**48**	**50**	**50**	**50**
Mean for males ≥ 200 cm[b]			127.7 ± 2.8	13.1 ± 0.3	9.9 ± 1.0	14.4 ± 0.4	5.0 ± 0.3	10.5 ± 0.5	9.2 ± 0.3	7.1 ± 0.3	10.9 ± 0.5
[max. value in brackets]			[139.3]	[14.0]	[13.7]	[15.7]	[5.8]	[12.2]	[10.2]	[8.1]	[12.5]

Variables: 1. bacular length; 2. proximal height; 3. proximal width; 4. distal height; 5. distal width; 6. proximal shaft height; 7. middle shaft height; 8. distal shaft height; 9. bacular mass.
[a] Number of bacula for canine aged animals. Sample size given in square brackets where this does not equal total sample size.
[b] Mean value of variable ± S.E. for the 7 largest males (≥ 200 cm) of unknown-age; maximum value in brackets.
* S.E. of one measurement can not be measured.

Table 5.3 *Growth in mean bacular length relative to mean standard body length*

Age group	Age (y)	*n*[a]	Mean bacular length[b] (mm)	Mean SBL[c] (cm)	Bacular length rel. to SBL[d]
Pup	< 1	3	28.5 ± 1.6	69.0 ± 2.5	4.1%
Yearling	1	5	47.8 ± 1.7	90.6 ± 2.7	5.3 %
Subadult	4	1*	86.6	137.0	–
	5	3	– [0]	– [0]	–
	6	2	102.2 [1*]	145.0 [1*]	–
	7	11	106.5 ± 3.0 [6]	159.8 ± 4.5 [6]	6.7% [6]
	4–7	**17**	**103.5 ± 3.3 [8]**	**155.1 ± 4.6 [8]**	**–**
Adult	8	8	110.0 ± 3.2 [7]	167.1 ± 7.1 [7]	6.6% [7]
	9	4	117.3 ± 3.8 [3]	171.0 ± 3.2 [3]	6.9% [3]
	10	3	117.8 ± 2.9	187.0 ± 1.7	6.3%
	8–10	**15**	**113.5 ± 2.2 [13]**	**172.6 ± 4.4 [13]**	**6.6%[13]**
	> 12	10	113.2 ± 4.3 [9]	185.9 ± 7.7 [9]	6.1% [9]
Total		**50**	**38**	**38**	**38**

[a] Number of canine aged animals with both bacular length and SBL recorded. Of the 50 canine aged animals, SBL was not recorded for 12 animals, i.e. $n = 38$. Sample size is given in square brackets where this does not equal total sample size.
[b] Bacular length (mean ± S.E.).
[c] Standard body length (mean ± S.E.). SBL is defined as the length from the nose to the tail in a straight line with the animal on its back.
[d] Bacular length (mm)/SBL (mm) × 100%.
* S.E. of one measurement can not be measured.

Bacular morphology

Bacular length and mass ranged from 26.6 to 139.3 mm and 0.1 to 12.5 g, respectively (Table 5.2).

The youngest animals in the sample were < 1 mo of age. In these individuals, the baculum was short, thin and rod-like, with no obvious distinction between the proximal and distal ends (Fig. 5.2). The shaft was slightly curved anteriorly (variable).

In yearlings, the baculum increased substantially in length and mass (Table 5.3). The distal end was slightly rounded but, there was no sign of bifurcation (Fig. 5.2).

In subadults, most bacula curved upwards at the distal end (i.e., superiorly). At the distal end of the baculum, there were two narrow projections (knobs): a well-developed ventral knob and a less prominent dorsal knob (Fig. 5.2). In older subadults, the ventral knob extended upwards and outwards forming a double knob (variable). The proximal end of the bacula was bulbous in all animals ≥ 4 y.

In adults 8 and 9 y of age the baculum was well-developed, with pronounced thickening of the proximal end (Fig. 5.2). At the bifurcated distal end, the ventral knob usually extended further than the dorsal knob. In older males, the baculum was more robust, but not necessarily longer. Small osseous growths were commonly found on the proximal end of the baculum ($n = 18$ subadult and adult bacula) creating a rough surface where the fibrous tissue of the *corpus cavernosum penis* attached. In some older specimens ($n = 16$ bacula), small knob-like growths (usually 1 or 2) were observed along the edge of the urethral groove, at the proximal ventral surface of the baculum.

Bacular length expressed in relation to SBL

Relative to SBL, bacular length increased rapidly in young animals, peaked at 9 y (6.9%), and then declined in animals ≥ 10 y, i.e., 6.3% (10 y); 6.1% (> 12 y) (Table 5.3). Relative growth patterns for subadults < 7 y could not be established because SBL was not available for all specimens (SBLs for 14 animals were not recorded, i.e., curve body lengths were recorded for seals measured in rough conditions at sea).

Bacular growth relative to age zero, RGR $\bar{y}_0$

Percent change in value of bacular measurement at age *t*, relative to value at age zero, is presented in Table 5.4.

In yearlings, bacular mass was the most rapidly growing variable, followed by bacular length, proximal height, distal height, proximal shaft height, proximal width and distal shaft height/middle shaft height. Distal width showed little sign of growth.

Growth of bacular variables continued to increase until at least 10 y, with bacular mass, middle shaft height and distal shaft height expressing continued growth in animals > 12 y. Bacular mass and distal height expressed greatest overall growth, followed by proximal height, proximal shaft height and bacular length (Table 5.4).

Bacular growth relative to the previous year, RGR $\bar{y}_{t-1}$

Percent change in value of bacular measurement at age *t*, relative to value at age *t*–1, for animals 7–10 y, is presented in Table 5.4. Percent increment in bacular length, distal height and bacular mass peaked at 8 y; middle shaft height and distal shaft height peaked at 9 y; proximal height, proximal width distal width and proximal shaft height peaked at 10 y.

Table 5.4 *Growth in bacular variables (1–9) relative to the mean value of bacular measurement: (i) at age zero, RGR* $\bar{y}_0$ *and (ii) from the previous year, RGR* $\bar{y}_{t-1}$. **Growth in SBL is also given. All measurements are in mm, apart from SBL (cm) and bacular mass (g).**

Age group	Age (y)	n[a]	SBL[b]	Var 1	Var 2	Var 3	Var 4	Var 5	Var 6	Var 7	Var 8	Var 9
Pup	< 1	3	–	–	–	–	–	–	–	–	–	–
Yearling	1	5	31	68	36	21	31	2	26	13	14	200
Subadult	4	1	99	204	106	89	227	68	149	150	128	2300
	5	3	– [0]	241	266	120	322	152	196	164	157	3300
	6	2	110 [1]	249	218	91	386	131	200	145	133	2950
	7	11	132; – [6]	256; 2.0	282; 20.4	118; 13.7	379; -1.5	143; 5.1	206; 2.0	186; 16.5	176; 18.8	3964; 33.2
Adult	8	8	142; 4.6 [7]	391; 9.9	341; 15.3	169; 23.4	448; 14.5	158; 6.3	239; 10.8	211; 8.9	191; 5.2	5600; 40.3
	9	4	148; 2.3 [3]	311; 4.9	304; -8.3	209; 14.9	453; 0.9	193; 13.4	243; 1.2	245; 10.9	225; 11.6	7125; 26.8
	10	3	171; 9.4	313; 0.8	447; 35.3	285; 24.7	491; 6.9	268; 25.8	346; 30.1	268; 6.6	234; 3.1	7533; 5.7
	> 12	10	169 [9]	297	343	189	495	196 [8]	320	290	241	8150
Total		**50**	**38**	**50**	**50**	**50**	**50**	**48**	**50**	**50**	**50**	**50**

Variables: 1. bacular length; 2. proximal height; 3. proximal width; 4. distal height; 5. distal width; 6. proximal shaft height; 7. middle shaft height; 8. distal shaft height; 9. bacular mass.
[a] Number of bacula for canine aged animals.
[b] SBLs for 12 of these animals were not recorded.
Values for growth relative to age zero are presented on the left hand side of the relevant columns, i.e., $[(\bar{y}_t - \bar{y}_0)/\bar{y}_0] \times 100\%$. Values for growth relative to the previous year are presented on the right hand side of the relevant columns, for animals 7–10 y of age, i.e., $[(\bar{y}_t - \bar{y}_{t-1})/\bar{y}_{t-1}] \times 100\%$.
Sample size given in square brackets where this does not equal total sample size.

Bacular length as an indicator of age

For animals 1–10 y, bacular length was highly, positively correlated with age (y) ($r = 0.83$, $n = 37$; Fig. 5.5a). However, after fitting the straight line model, the plot of the residuals versus fitted values was examined, and the straight line model was found to be inadequate (the residuals were not scattered randomly about zero, see Weisberg, 1985, p. 23). Thus, bacular length could not be used as a reliable indicator of absolute age.

For the range of ages available in this study, the coefficient of variation in bacular length for young males 1–5 y (36.8%) was considerably higher than in older males (8–10 y, 6.6%; > 12 y, 10.7%) Table 5.2.

Although bacular length was not a good indicator of absolute age, it was a ‘rough indicator’ of age group. When bacular length is known, the following linear discriminant functions can be used to categorise each observation into one of four age groups (pups, yearlings, subadult, adults):

$$y_0 = -5.50 + 0.39x$$
$$y_1 = -15.53 + 0.65x$$
$$y_2 = -67.25 + 1.35x$$
$$y_3 = -87.77 + 1.54x$$

where x = bacular length (mm); subscript 0 = pup; subscript 1 = yearling; subscript 2 = subadult; and subscript 3 = adult. The seal is classified into the age group associated with the linear discriminant function which results in the minimum value. Of the 50 observations in this study, 86% were correctly classified using this method (Table 5.5).

Bacular length as an indicator of SBL

Bacular length was highly, positively correlated with SBL ($r = 0.88$, $n = 86$; Fig. 5.3a). When bacular length is known, the following equation (linear least squares fit; untransformed data) can be used as a ‘rough indicator’ of SBL:

$$y = 36.42 + 1.24x$$

which may equivalently be written as SBL = $e^{36.42} \times$ bacular length$^{1.24}$, where the S.E. of the intercept is 4.98 and the S.E. of the slope is 0.05 ($n = 86$).

Bivariate allometric regression

With one exception, bacular variables were significantly, positively correlated with each other, $r \geq 0.7$ (Table 5.6). Distal width with proximal width ($r = 0.67$) was the only exception.

Value of bacular measurement on SBL

Of the 103 seals in the study, 86 were used in regression analysis for log of baculum measurement on log SBL, i.e., all pups ($n = 3$) were excluded from regression analysis, and SBLs for 14 animals were not recorded.

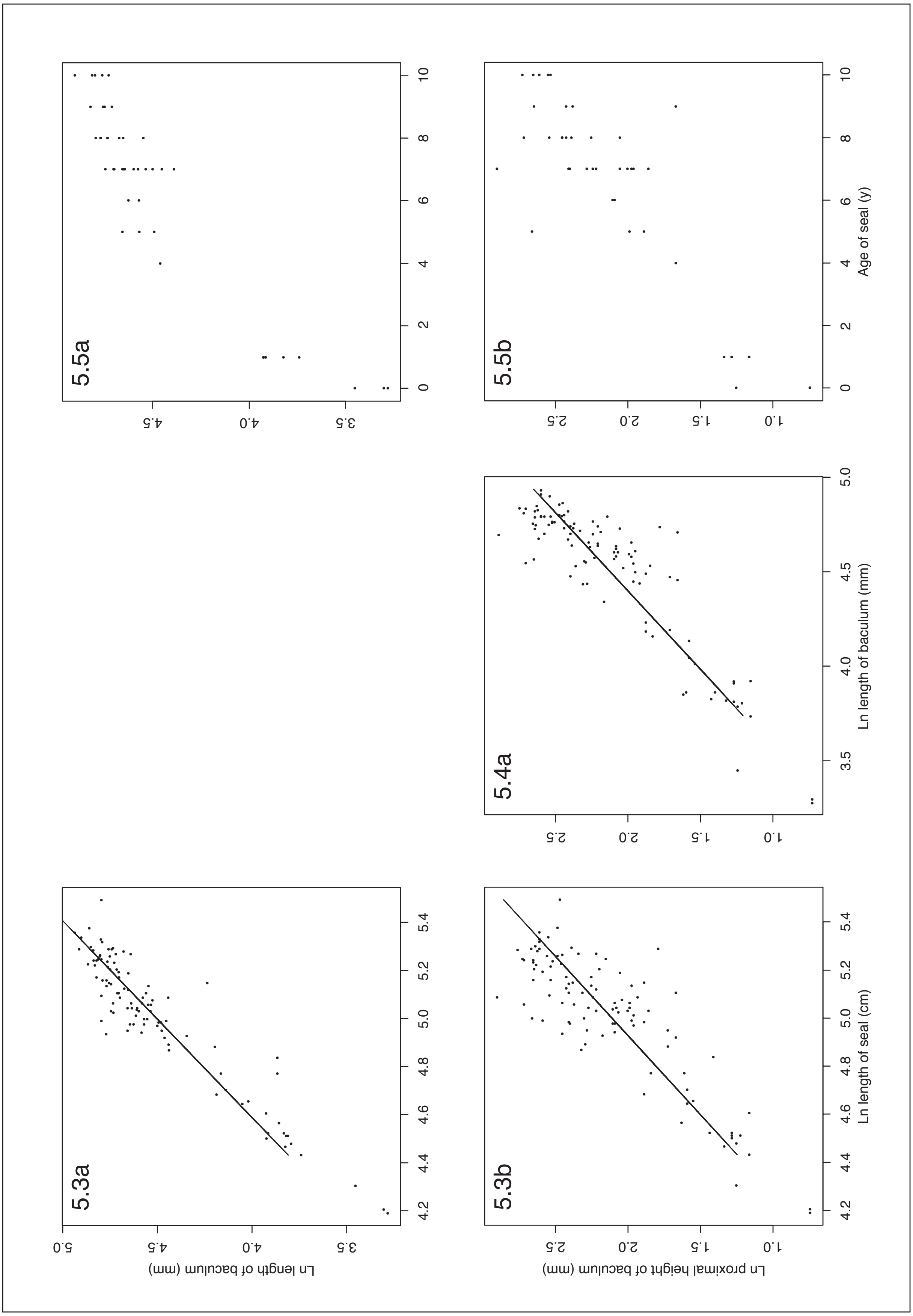

Fig. 5.3a, 5.3b Bivariate plot of log baculum measurement (mm) on log length of seal (cm).
Fig. 5.4a Bivariate plot of log baculum measurement (mm) on log length of baculum (mm).
Fig. 5.5a, 5.5b Bivariate plot of log baculum measurement (mm) on age of seal (y).

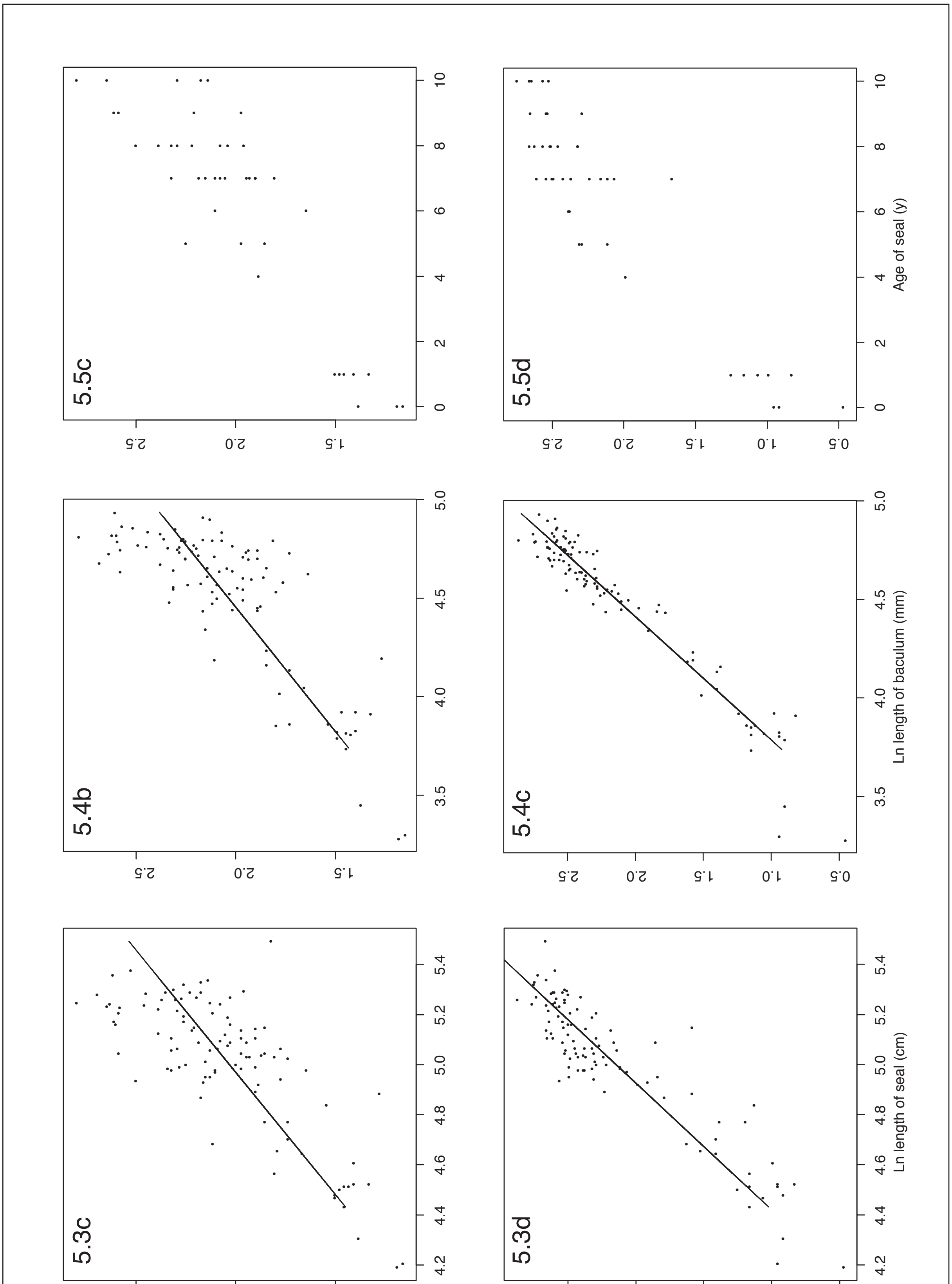

Fig. 5.3c, 5.3d Bivariate plot of log baculum measurement (mm) on log length of seal (cm).
Fig. 5.4b, 5.4c Bivariate plot of log baculum measurement (mm) on log length of baculum (mm).
Fig. 5.5c, 5.5d Bivariate plot of log baculum measurement (mm) on age of seal (y).

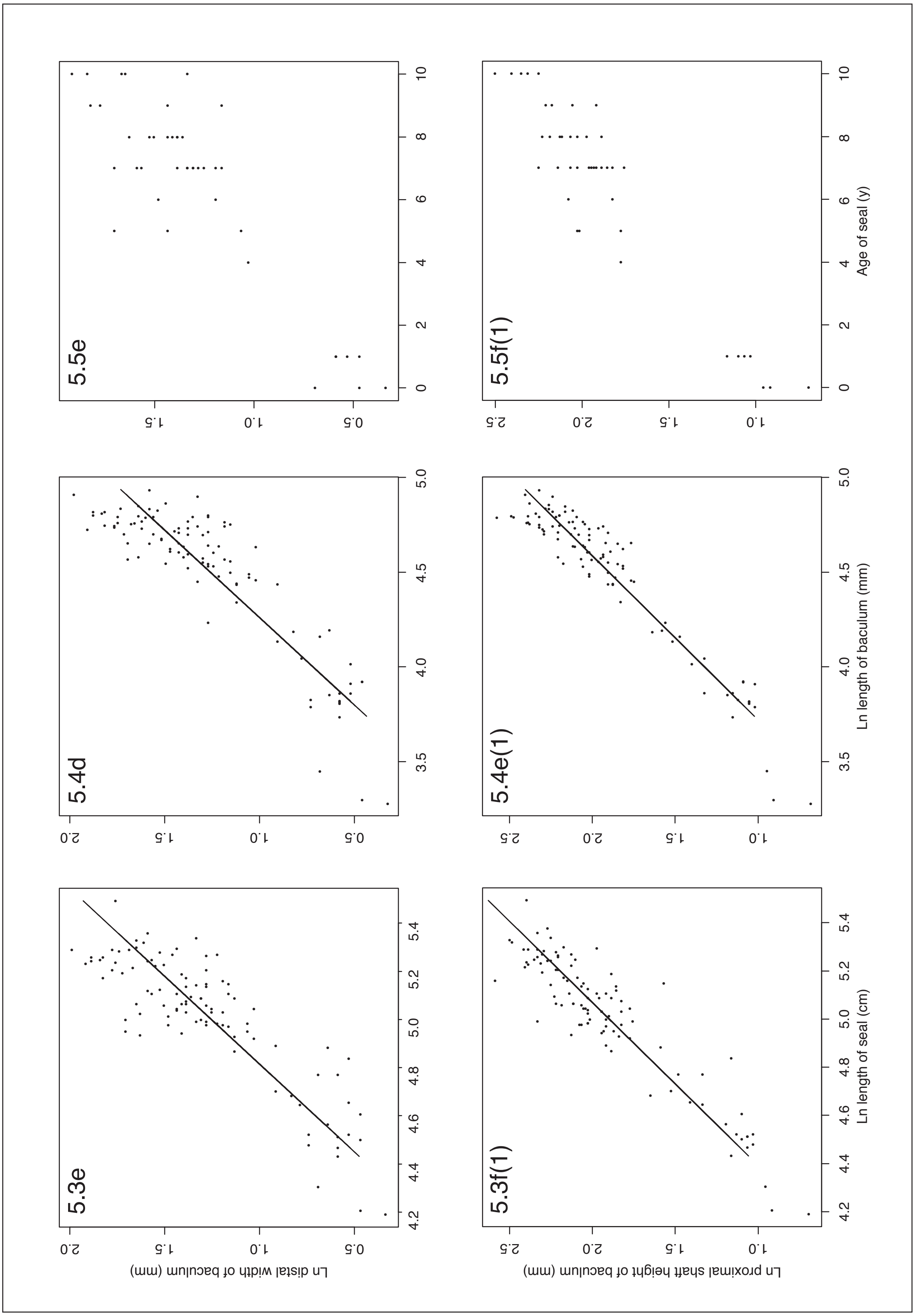

Fig. 5.3e, 5.3f(1) Bivariate plot of log baculum measurement (mm) on log length of seal (cm).
Fig. 5.4d, 5.4e(1) Bivariate plot of log baculum measurement (mm) on log length of baculum (mm).
Fig. 5.5e, 5.5f(1) Bivariate plot of log baculum measurement (mm) on age of seal (y).

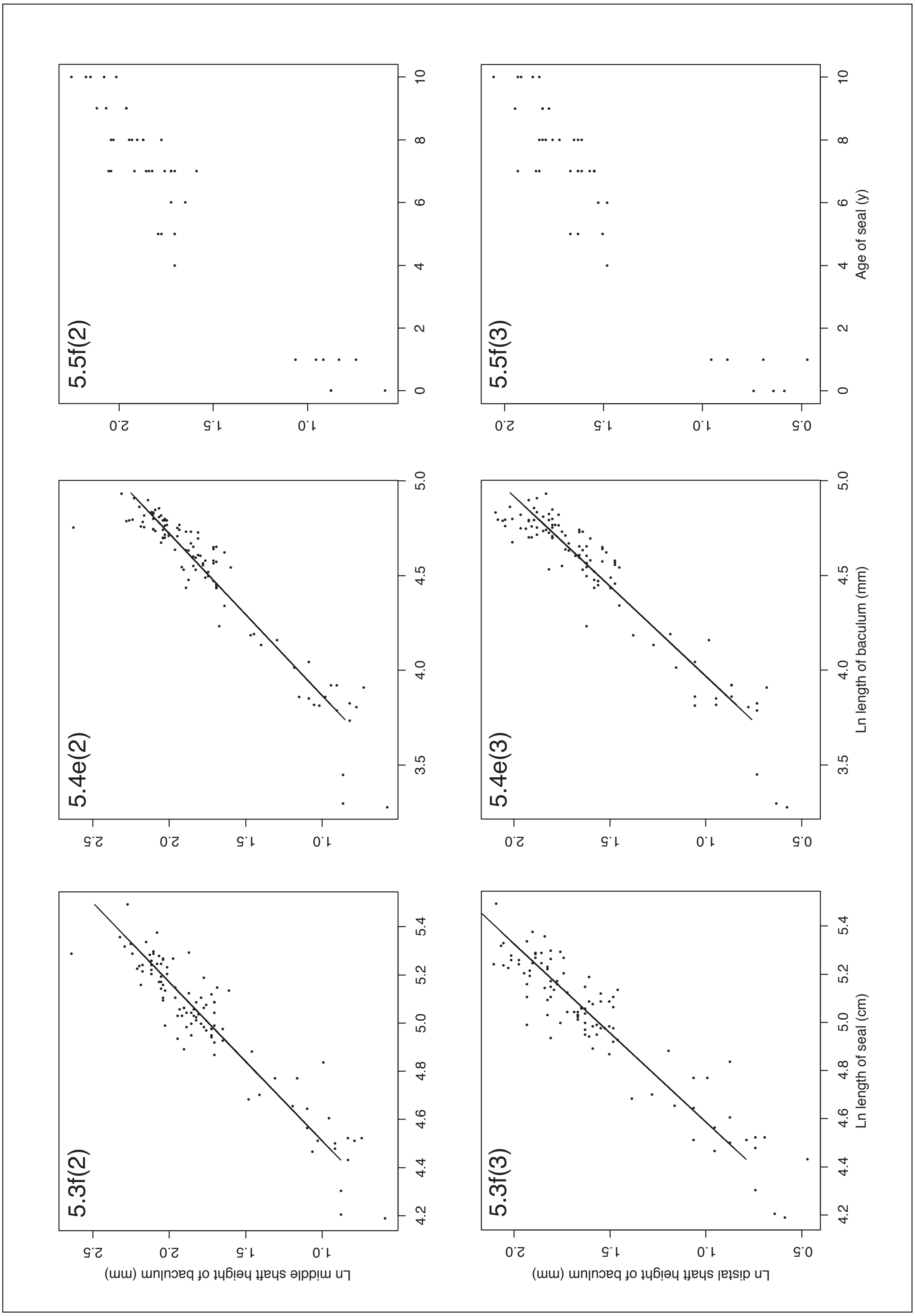

Fig. 5.3f(2), 5.3f(3) Bivariate plot of log baculum measurement (mm) on log length of seal (cm).
Fig. 5.4e(2), 5.4e(3) Bivariate plot of log baculum measurement (mm) on log length of baculum (mm).
Fig. 5.5f(2), 5.5f(3) Bivariate plot of log baculum measurement (mm) on age of seal (y).

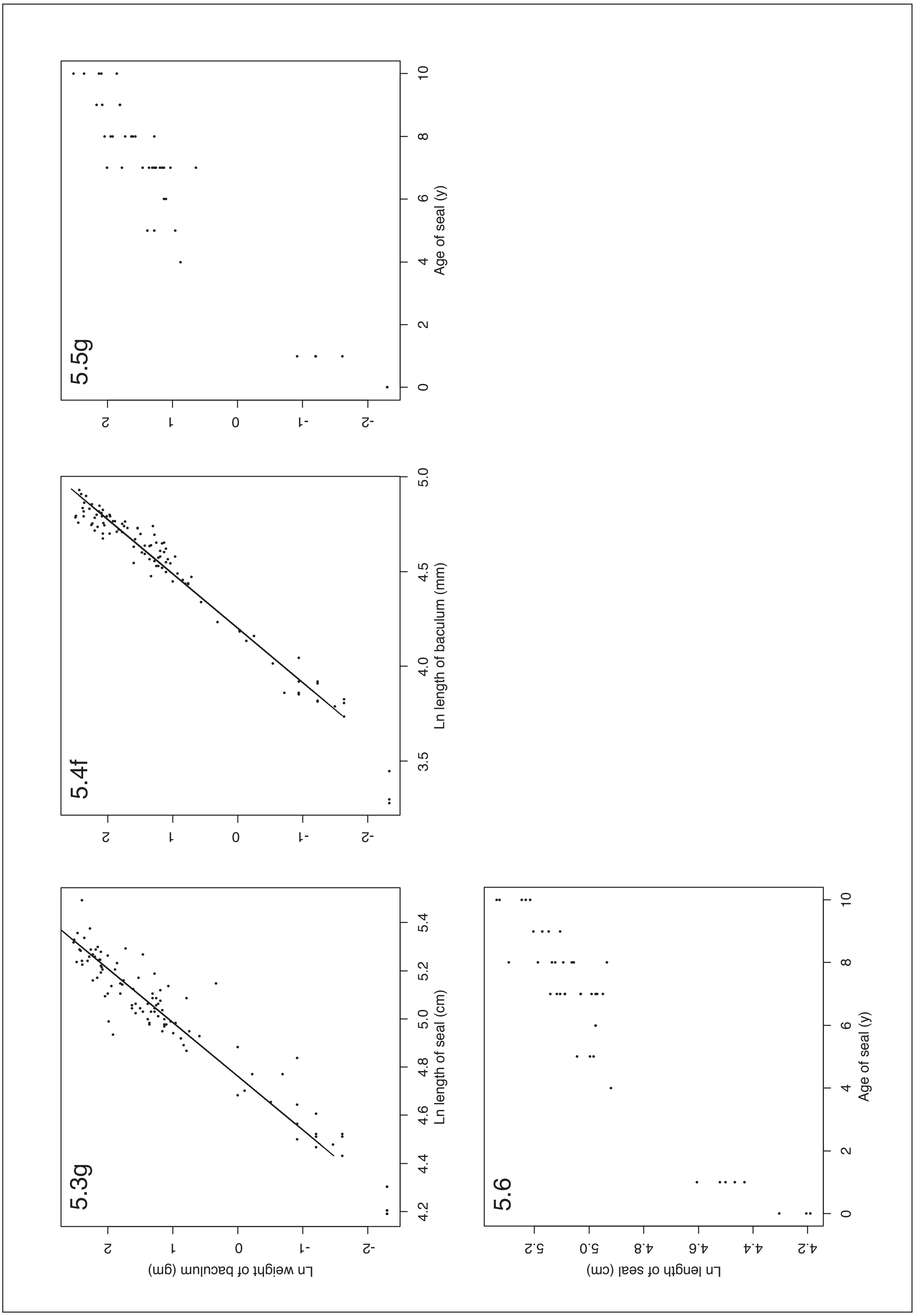

Fig. 5.3g Bivariate plot of log baculum measurement (mm) on log length of seal (cm).
Fig. 5.4f Bivariate plot of log baculum measurement (mm) on log length of baculum (mm).
Fig. 5.5g Bivariate plot of log baculum measurement (mm) on age of seal (y).
Fig 5.6 Bivariate plot of log length of seal (cm) on age of seal (y).

There was little difference between the ordinary least square straight lines fitted to the data, and the 'robust' least squares straight lines fitted to the data. The 'robust' straight line equations for regressing log of baculum measurement on log of seal length are given in Table 5.7.

All bacular variables were highly, positively correlated with SBL, $r \geq 0.7$ (Fig. 5.3a–g; Table 5.7). Proximal width ($r = 0.68$) was the only exception.

Relative to SBL, growth in distal height, distal width, proximal shaft height, distal shaft height and bacular mass was positively allometric; and proximal width was isometric (Table 5.7). Regression slopes for bacular length, proximal height and middle shaft height scaled with positive slope (Table 5.7).

Value of bacular measurement on bacular length

Of the 103 seals in the study, 100 were used in regression analysis for log of baculum measurement on bacular length, i.e., all pups ($n = 3$) were excluded from regression analysis.

All bacular variables were highly, positively correlated with bacular length, $r \geq 0.7$ (Fig. 5.4a–f; Table 5.8).

Relative to bacular length, growth in distal height, proximal shaft height and proximal height was positively allometric relative to bacular length; distal width and distal shaft height was isometric; and proximal width was negatively allometric (Table 5.8). Regression slopes for middle shaft height and bacular mass scaled with positive slope (Table 5.8). The slope for bacular mass was considerably steeper than for other variables.

Value of bacular measurement on age

Of the 40 seals aged from upper canines, 37 were used in regression analysis for log of baculum measurement versus age, i.e., all pups ($n = 3$) were excluded from regression analysis.

Overall, the plots of log bacular measurements versus log SBL were better described by linear relationships than the plots of log bacular measurements versus age, even though the assoc-iated correlation coefficients were moderately to strongly positive (see Griffiths *et al.*, 1998, p. 126) (Fig. 5.5a–g; Table 5.9). Proximal height was the only variable that roughly resembled a straight line (Fig. 5.5b). All variables scaled with negative slope relative to age.

Table 5.5 *Discriminant analysis for seal age group (pup, yearling, subadult, adult) inferred from bacular length*

Known age group	***n*[a]**	**Classification into age group**			
		0	**1**	**2**	**3**
		Pup (< 1 mo)	Yearling (7 mo to 1 y 6 mo)	Subadult (1 y 7 mo to 7 y 6 mo)	Adult[b] (≥ 7 y 7 mo)
0	**3**	3 (100%)	0	0	0
1	**5**	0	5 (100%)	0	0
2	**17**	0	0	14 (82%)	4
3	**25**	0	0	3	21 (84%)
Total	**50**	**3**	**5**	**17**	**25**

[a] Number of animals aged from counts of incremental lines observed in the dentine of upper canines, $n = 50$. Percentage of animals correctly classified into age group is given in brackets.
[b] Included animals > 12 y.

Table 5.6 *Spearman rank-order correlation coefficients for log bacular variables*

	Var 1	**Var 2**	**Var 3**	**Var 4**	**Var 5**	**Var 6**	**Var 7**	**Var 8**	**Var 9**
Var 1	1.00	0.82	0.71	0.90	0.80	0.88	0.92	0.90	0.95
Var 2	0.82	1.00	0.80	0.76	0.75	0.85	0.84	0.80	0.85
Var 3	0.71	0.80	1.00	0.69	*0.67*	0.76	0.75	0.70	0.77
Var 4	0.90	0.76	0.69	1.00	0.80	0.86	0.89	0.88	0.92
Var 5	0.80	0.75	*0.67*	0.80	1.00	0.79	0.80	0.80	0.83
Var 6	0.88	0.85	0.76	0.86	0.79	1.00	0.94	0.89	0.94
Var 7	0.92	0.84	0.75	0.89	0.79	0.94	1.00	0.96	0.97
Var 8	0.90	0.80	0.70	0.88	0.80	0.89	0.96	1.00	0.95
Var 9	0.95	0.85	0.77	0.92	0.83	0.94	0.97	0.95	1.00
Total	**103**	**103**	**103**	**103**	**101**[a]	**103**	**103**	**103**	**103**

Variables: 1. bacular length; 2. proximal height; 3. proximal width; 4. distal height; 5. distal width; 6. proximal shaft height; 7. middle shaft height; 8. distal shaft height; 9. bacular mass.
[a] Two distal width measurements were not recorded, i.e., PEM2049 and PEM2134.
All correlations are significant at the 1% level (2-tailed), i.e., $P = 0.00$.

Table 5.7 ***'Robust' least squares straight line equations, Spearman rank-order correlation coefficients and allometry for log bacular measurement (mm) on log seal body length (cm)***

Dependent variable	Linear regression				Allometry		
	n^a	Intercept ± S.E.	Slope ± S.E.	r (p-values)	Alternative hypothesis	*d.f.*	p-value
1. Length of baculum	86	-1.67 ± 0.22	1.23 ± 0.04	0.88 (0.00)	NA	NA	NA
2. Proximal height	86	-5.58 ± 0.45	1.54 ± 0.09	0.78 (0.00)	NA	NA	NA
3. Proximal width	86	-3.12 ± 0.48	1.03 ± 0.09	0.68 (0.00)	$H_1 : \hat{\beta} \neq 1$	84	0.78*
4. Distal height	86	-7.88 ± 0.46	2.00 ± 0.09	0.84 (0.00)	$H_1 : \hat{\beta} > 1$	84	0.00
5. Distal width	84[b]	-5.64 ± 0.04	1.38 ± 0.09	0.80 (0.00)	$H_1 : \hat{\beta} > 1$	82[b]	0.00
6. Proximal shaft height	86	-5.59 ± 0.29	1.50 ± 0.06	0.87 (0.00)	$H_1 : \hat{\beta} > 1$	84	0.00
7. Middle shaft height	86	-5.92 ± 0.28	1.53 ± 0.06	0.90 (0.00)	NA	NA	NA
8. Distal shaft height	86	-5.24 ± 0.29	1.36 ± 0.06	0.87 (0.00)	$H_1 : \hat{\beta} > 1$	84	0.00
9. Mass of baculum	86	-21.51 ± 0.68	4.51 ± 0.13	0.91 (0.00)	$H_1 : \hat{\beta} > 1$	84	0.00
Total	**86**						

[a] Number of bacula for canine aged animals and animals of unknown-age (the 3 pups were excluded from analysis, and SBLs from 14 males were not recorded, i.e., $n = 86$ bacula).
[b] Two distal width measurements were not recorded for PEM2049 and PEM2134.
r, Spearman rank-order correlation coefficient.
All correlations are significant at the 1% level (2-tailed).
NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable.
* Since the p-value was > 0.05, we cannot reject H_0 in favour of H_1 at the 5% significance level; therefore growth is isometric.

Table 5.8 ***'Robust' least squares straight line equations, Spearman rank-order correlation coefficients and allometry for log bacular measurement (mm) on log bacular length (mm)***

Dependent variable	Linear regression				Allometry		
	n^a	Intercept ± S.E.	Slope ± S.E.	r (p-values)	Alternative hypothesis	*d.f.*	p-value
2. Proximal height	100	-3.11 ± 0.26	1.21 ± 0.06	0.80 (0.00)	$H_1 : \hat{\beta} > 1$	98	0.00
3. Proximal width	100	-1.52 ± 0.29	0.79 ± 0.06	0.69 (0.00)	$H_1 : \hat{\beta} < 1$	98	0.00
4. Distal height	100	-5.07 ± 0.18	1.60 ± 0.04	0.89 (0.00)	$H_1 : \hat{\beta} > 1$	98	0.00
5. Distal width	98[b]	-3.61 ± 0.26	1.08 ± 0.06	0.79 (0.00)	$H_1 : \hat{\beta} \neq 1$	96[b]	0.15*
6. Proximal shaft height	100	-3.30 ± 0.17	1.16 ± 0.04	0.87 (0.00)	$H_1 : \hat{\beta} > 1$	98	0.00
7. Middle shaft height	100	-3.52 ± 0.15	1.17 ± 0.03	0.91 (0.00)	NA	NA	NA
8. Distal shaft height	100	-3.18 ± 0.29	1.05 ± 0.04	0.89 (0.00)	$H_1 : \hat{\beta} \neq 1$	98	0.15*
9. Mass of baculum	100	-14.66 ± 0.29	3.49 ± 0.06	0.94 (0.00)	NA	NA	NA
Total	**100**						

[a] Number of bacula for canine aged animals and animals of unknown-age (the 3 pups were excluded from analysis, i.e., $n = 100$ bacula).
[b] Two distal width measurements were not recorded for PEM2049 and PEM2134.
r, Spearman rank-order correlation coefficient.
All correlations are significant at the 1% level (2-tailed).
NA, model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test not applicable.
* Since the p-value was > 0.05, we cannot reject H_0 in favour of H_1 at the 5% significance level; therefore growth is isometric.

Table 5.9 ***'Robust' least squares straight line equations and Spearman rank-order correlation coefficients for log bacular measurement (mm) on age (y)***

Dependent variable	Linear regression			
	n^a	Intercept ± S.E.	Slope ± S.E.	r (p-values)
1. Length of baculum	37	3.88 ± 0.05	0.10 ± 0.01	0.83 (0.00)
2. Proximal height	37	1.13 ± 0.08	0.15 ± 0.01	0.67 (0.00)
3. Proximal width	37	1.31 ± 0.09	0.11 ± 0.01	0.78 (0.00)
4. Distal height	37	1.10 ± 0.10	0.17 ± 0.01	0.76 (0.00)
5. Distal width	37	0.45 ± 0.07	0.13 ± 0.01	0.68 (0.00)
6. Proximal shaft height	37	1.05 ± 0.06	0.13 ± 0.01	0.74 (0.00)
7. Middle shaft height	37	0.89 ± 0.06	0.13 ± 0.01	0.85 (0.00)
8. Distal shaft height	37	0.82 ± 0.06	0.11 ± 0.01	0.79 (0.00)
9. Mass of baculum	37	-1.28 ± 0.15	0.37 ± 0.02	0.87 (0.00)
Total	**37**			
Standard body length	**26**[b]	4.46 ± 0.04	0.08 ± 0.01	0.83 (0.00)

[a] Number of bacula for canine aged animals (only animals 1–10 y were included in analysis, i.e., $n = 37$ bacula).
[b] SBLs for 11 aged males 1–10 y were not recorded.
r, Spearman rank-order correlation coefficient.
All correlations are significant at the 1% level (2-tailed).
[Model assumptions required to test hypotheses about the slope of the line (b) were not met, i.e., test for allometry not applicable].

DISCUSSION

Bacular size

In Cape fur seals from the Eastern Cape coast, maximum bacular length was 139.3 mm and mass was 12.5 g; however bacula up to 141 mm (Oosthuizen & Miller, 2000) and 16.8 g (Rand, unpubl. report) have been reported from other areas. Baculum length was similar to that of the northern fur seal (Scheffer, 1950). As with other Otariidae, bacular length was considerably smaller than that of most Phocidae and the Odobenidae (Scheffer & Kenyon, 1963).

Bacular shape

Although detailed information on the morphology of the otariid bacula is sparse, bacular shape was most similar to *Callorhinus* and *Zalophus* (Kim *et al*., 1975; Morejohn, 1975; King, 1983). For example, in *Arctocephalus*, *Callorhinus* and *Zalophus*, the adult bacular apex consists of a dorsal and a ventral knob. When viewed anteriorly, the knobs are parallel sided (*Arctocephalus* and *Zalophus*), or resemble a figure-of-eight (*Callorhinus*).

Apical keels (lateral expansion of the apex) are present on the baculum of some *Zalophus*, yet absent in both *Arctocephalus* and *Callorhinus* (Kim *et al*., 1975; Morejohn, 1975).

Bacular length as an indicator of SBL and age

As with other species of pinnipeds, there is considerable variation in bacular length with age, especially in younger animals (Rand, unpubl. report; Scheffer, 1950; Bester, 1990; Oosthuizen & Miller, 2000).

In male Cape fur seals, bacular length was found to be a 'rough indicator' of SBL and age group, but not of absolute age. The classification criteria for age group, and SBL, developed in this study will be particularly useful when canines are not available for age determination; a seal is decomposed/scavenged (total SBL can not be measured); the skull is incomplete/absent (total SBL can not be extrapolated from skull length); or museum records have been misplaced or destroyed. As more specimens become available, the classification criteria will be more precise.

Bacular growth

In male Cape fur seals, growth of the baculum is a differential process with most variables growing rapidly relative to SBL and bacular length. Two variables were isometric and one was negatively allometric, relative to bacular length, indicating that the adult baculum was not simply an enlarged version of the juvenile baculum.

Growth changes in bacular length and mass described in this study generally support findings reported by Oosthuizen & Miller (2000). In this study based primarily on animals collected from the south and south-west coast of southern Africa, growth in bacular length took place rapidly up until 5 y; peaked at 9–10 y; and then slowed. Our findings could not be compared to those of Rand (1956) because, in the latter, age was estimated from cranial suture closure which has subsequently been shown to be an unreliable indicator of absolute age in this species (Stewardson *et al*., 200X*b*).

The biological significance of bacular growth patterns

In male Cape fur seals, a growth spurt in bacular length occurs at 2–3 y (Rand, unpubl. report; Oosthuizen & Miller, 2000), when males attain puberty (Stewardson *et al*., 1998). After puberty, the baculum continues to increase in length with increasing age, approximating full length at about 9 y (Oosthuizen & Miller, 2000; present study). Bacular dimensions, other than length, approximate full size between 8–10 y (present study), when most males have attained full reproductive capacity (present study). Although males can sire offspring at a young age (e.g., at 4 y in captivity; Linda Clokie-Van Zyl, pers. comm.), bacular growth is geared to coincide with the attainment of social maturity, presumably to enhance the effective-ness of copulation.

Socially mature male Cape fur seals: (i) may achieve a high level of polygyny at large colonies (David, 1987); (ii) usually copulate once with each harem female, 5–7 days postpartum during a brief breeding season (November to late December) (David & Rand, 1986); and (iii) usually exhibit brief intromission duration (Stewardson, pers. obs.). In such males, the baculum is therefore large enough to provide sufficient mechanical support for insertion and repeated copulations (with potentially numerous females within a short period of time), and may assist in deeper penetration. The ornate apex presumably serves to stimulate the females vagina (e.g., Eberhard, 1985, 1996); however, considering that: (i) female Cape fur seals are not 'induced ovulaters'; (ii) copulation occurs when the female is sexually receptive; and (iii) sperm competition is weak, the function of the apex in this species remains unclear.

CONCLUSION

Data presented in this study provide detailed information on the morphology of the Cape fur seal bacula, confirming earlier descriptions given by Mohr (1963) and Rand (1956; unpubl. report). They provide new information on the patterns of bacular growth in relation to age and SBL (Rand, 1956; Oosthuizen & Miller, 2000), and demonstrate that bacular length is a 'rough indicator' of SBL and age group, but not of absolute age.

Further studies examining the morphology and growth patterns of the pinniped bacula from known-age animals are required to establish species affinities, and understand the significance of bacular variation in relation to copulatory behaviour and mating systems.

ACKNOWLEDGEMENTS

We wish to express our sincere appreciation to the following persons and organisations for assistance with this study: Dr V. Cockcroft (Port Elizabeth Museum), Dr J. Hanks (WWF-South Africa) and Prof. A. Cockburn (Australian National University) for financial and logistic support; Mr B. Rose (Oosterlig Visserye, Port Elizabeth) who enabled us to collect seals from his commercial fishing vessels; staff of the Port Elizabeth Museum for use of bacula (n = 29) collected before 1992, especially Dr A. Batchelor, Dr G. Ross and Dr V. Cockcroft; Dr J.H.M David and Mr H. Oosthuizen (Marine Cosatal Management, Cape Town) for assistance with age determination; Mr N. Minch (Australian National University) for photographic editing; Dr C. Groves and Dr A. Thorne (Australian National University) for their constructive comments on an earlier draft of this manuscript. This paper is part of a larger study on behalf of the World Wild Fund For Nature – South Africa (project ZA-348, part 1c).

REFERENCES

BESTER MN (1990) Reproduction in the male sub-Antarctic fur seal *Arctocephalus tropicalis. Journal of Zoology* (London) **222**, 177–185.

BURT WH (1939) A study of the baculum in the genera *Perognathus* and *Dipodomys. Journal of Mammalogy* **17**, 145–156.

CHAINE J (**1925/26**) L'Os pénien, étude descriptive et comparative. *Actes Societe Linnéenne de Bordeaux* **78**, 5–195.

COCHRAN WG (1977) *Sampling techniques*, 3rd edn, New York: John Wiley & Sons.

DAVID JHM (1987) South African fur seal *Arctocephalus pusillus pusillus*. In *Status, biology and ecology of fur seals*: Proceedings of an international workshop, Cambridge, England 23–27 April 1984 (ed. Croxall JP and Gentry RL) *NOAA Tech. Rep. NMFS* **51**, 65–71.

DAVID JHM, RAND RW (1986) Attendance behaviour of South African fur seals. In *Fur seals: Maternal strategies on land and at sea*: (ed. Gentry RL, Kooyman GL), pp. 126–141. Princeton: Princeton University Press.

DIXSON AF (1995) Baculum length and copulatory behaviour in carnivores and pinnipeds (Grand Order Ferae). *Journal of Zoology* (London) **235**, 67–76.

EBERHARD WG (1985) *Sexual selection and animal genitalia*. Cambridge, Massachusetts: Harvard University Press.

EBERHARD WG (1996) *Female control: sexual selection by cryptic female choice*. Princeton, New Jersey: Princeton University Press.

ELDER WH (1951) The baculum as an age criterion in mink. *Journal of Mammalogy* **32**, 43–50.

EWER RF (1973) *The carnivores*. New York: Cornell University Press.

GIBBONS JD, CHAKRABORTI S (1992) *Nonparametric statistical inference*, 3rd edn, New York: Marcel Dekker, Inc.

GRIFFITHS D, STIRLING WD, WELDON KL (1998) *Understanding data. Principles & practice of statistics*. New York: John Wiley and Sons.

HAMILTON JE (1939) A second report on the Southern Sea Lion *Otaria byronia* (de Blainville). *Discovery Report* **19**, 121–164.

HEWER HR (1964) The determination of age, sexual maturity and a life-table in the grey seal (*Halichoerus grypus*). *Proceedings. Zoological Society of London* **142**, 593–624.

KIM KC, REPENNING CA, MOREJOHN GV (1975) Specific antiquity of the sucking lice and evolution of otariid seals. *Rapports et Proces-Verbaux des Reunions. Conseil International pour I'Exploration de la Mer* **169**, 544–549.

KING JE (1983) *Seals of the World*, 2nd edn, London: British Museum (Nat. Hist.), Oxford University Press.

LAWS RM (1956) The elephant seal (*Mirounga leonina* Linn.). III. The physiology of reproduction. *Falkland Islands Dependencies Survey. Scientific Reports* **15**, 1–66.

LAWS RM, SINHA A A (1993) Reproduction. In *Handbook on Antarctic seal research methods and techniques* (ed. Laws RM), pp. 228–267. Cambridge: Cambridge University Press.

LEE MR, SCHMIDLY DJ (1977) A new species of Peromyscus (Rodentia: Muridae) from Coahuila, Mexico. *Journal of Mammalogy* **58**, 263–268.

LONG CA, FRANK T (1968) Morphometric variation and function in the baculum, with comments on correlation of parts. *Journal of Mammalogy* **49**, 32–43.

MAYR E (1963) *Animal species and evolution*. Cambridge: Belknap Press.

MCLAREN IA (1960) Are the Pinnipedia biphyletic? *Systematic Zoology* **9**, 18–28.

MILLER EH (1974) Social behaviour between adult male and female New Zealand fur seals, *Arctocephalus forsteri* (Lesson) during the breeding season. *Australian Journal of Zoology* **22**, 155–173.

MILLER EH, PONCE DE LEÓN A, DELONG RL (1996) Violent interspecific sexual behaviour by male sea lions (Otariidae): evolutionary and phylogenetic implications. *Marine Mammal Science* **12**, 468–476.

MILLER EH, STEWART ARJ, STENSON GB (1998) Bacular and testicular growth, allometry, and variation in the harp seal (*Pagophilus groenlandicus*). *Journal of Mammalogy* **79**, 502–513.

MILLER EH, JONES, IL, STENSON, GB (1999) Baculum and testes of the hooded seal (*Cystophora cristata*): growth and size-scaling and their relationships to sexual selection. *Canadian Journal of Zoology* **77**, 470–470.

MOHR E (1963) Os penis und Os clitoridis der Pinnipedia. *Zeitschrift für Säugetierkunde* **28**, 19–37.

MOREJOHN GV (1975) A phylogeny of otariid seals based on morphology of the baculum. *Rapports et Proces-Verbaux des Reunions. Conseil International pour I'Exploration de la Mer* **169**, 49–56.

OOSTHUIZEN WH (1997). Evaluation of an effective method to estimate age of Cape fur seals using ground tooth sections. *Marine Mammal Science* **13**, 683–693.

OOSTHUIZEN WH, MILLER EH (2000). Bacular and testicular growth and allometry in the Cape fur seal (*Arctocephalus p. pusillus*). *Marine Mammal Science* **16**, 124–140.

PATTERSON BD (1983) Baculum-body size relationships as evidence for a selective continuum on bacular morphology. *Journal of Mammalogy* **64**, 496–499.

PATTERSON BD, THAELER CS-JR (1982) The mammalian baculum: hypotheses on the nature of bacular variability. *Journal of Mammalogy* **63**, 1–15.

RAND RW (1949) Studies on the Cape fur-seal (*Arctocephalus pusillus*, Schreber) 3: Age-grouping in the male. Union of South Africa Department of Agriculture. Government Guano Island Administration (unpublished report).

RAND RW (1956) The Cape fur seal *Arctocephalus pusillus* (Schreber). Its general characteristics and moult. Union of South Africa Department of Commerce and Industry, Division of Sea Fisheries Investigational Report 21.

SCHEFFER VB (1950) Growth of the testes and baculum in the fur seal, *Callorhinus ursinus. Journal of Mammalogy* **31**, 384–394.

SCHEFFER VB, KENYON KW (1963) Baculum size in pinnipeds. *Zeitschrift für Säugetierkunde* **28**, 38–41.

STEWARDSON CL, BESTER MN, OOSTHUIZEN WH (1998) Reproduction in the male Cape fur seal *Arctocephalus pusillus pusillus*: age at puberty and annual cycle of the testis. *Journal of Zoology* (*London*) **246**, 63–74.

STEWARDSON CL, PRVAN T, MEŸER M (200X*a*). Age determination and growth in the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): part one, external body measurements. *Journal of Anatomy* (*Cambridge*) (submitted 2001).

STEWARDSON CL, PRVAN T, MEŸER M (200X*b*). Age determination and growth in the male Cape fur seal *Arctocephalus pusillus pusillus* (Pinnipedia: Otariidae): part two, skull. *Journal of Anatomy* (*Cambridge*) (submitted 2001).

SUTTON DA, NADLER CF (1974) Systematic revision of three Townsend chipmunks (*Eutamias townsendii*). *Southwestern Naturalist*, **19**, 199–212.

WEISBERG S (1985) *Applied linear regression*, 2nd edn, New York: John Wiley & Sons.

Appendix 5.1 ***Cape fur seals (n = 103) examined in this study.*** **Animals were collected from the Eastern Cape coast of South Africa between August 1978 and December 1995.**

	ID No.	Date of collection	Approximate location[b]	Method of collection[c]	SBL (cm)
1.	PEM603	2 Aug 78	Bell Buoy, Algoa Bay (AB) (33° 59'S, 25° 42'E)	sci. permit	150
2.	PEM605	4 Apr 79	Riy Bank, AB (34° 00'S, 25° 53'E)	sci. permit	153
3.	PEM607	30 Sep 79	King's Beach, Port Elizabeth (PE) (33° 58'S, 25° 39'E)	rehab. (D)	91
4.	PEM608	29 Aug 79	Cape Recife–Riy Bank, AB (34° 02'S, 25° 42'E – 34° 00'S, 25° 53'E)	sci. permit	182
5.	PEM661	17 July 74	Riy Bank–St. Croix, AB (34° 00'S, 25° 53'E – 33° 48'S, 25° 46'E)	sci. permit	141
6.	PEM670	5 Mar 79	King's Beach, PE (33° 58'S, 25° 39'E)	stranding	158
7.	PEM676	16 Feb 81	NR	oceanarium	197
8.	PEM824	23 Mar 82	Pollock Beach, PE (33° 59'20"S, 25° 40'30"E)	stranding	174
9.	PEM828	26 Mar 82	Port Elizabeth Harbour (33° 58'S, 25° 37'E)	stranding	158
10.	PEM834	21 Apr 82	22 km E of Sundays River Mouth, Woody Cape (WC)	stranding	162
11.	PEM874	18 Oct 82	32 km E of Sundays River Mouth, WC	stranding	157
12.	PEM877	2 Oct 82	E of Swartkops River Mouth, AB	stranding	165
13.	PEM888	2 Nov 82	7 km E of Kasuga River Mouth, Port Alfred (PA)	stranding	212
14.	PEM889	2 Nov 82	4 km E of Kasuga River Mouth, PA	stranding	138
15.	PEM898	22 Dec 82	1 km E of Van Starden's River Mouth, St. Francis Bay (FB)	stranding	200
16.	PEM916	Jan 1983	Willows, PE (34° 03'S, 25° 35'E)	stranding	91
17.	PEM917	11 Jan 83	2 km W of Maitland River Mouth, FB	stranding	104
18.	PEM928	14 Mar 82	28 km E of Sundays River Mouth, WC	stranding	140
19.	PEM951	16 May 83	35 km E of Sundays River Mouth, WC	stranding	170
20.	PEM952[a]	22 Feb 80	King's Beach, PE (33° 58'S, 25° 39'E)	stranding	243
21.	PEM958	13 Dec 83	Humewood, PE (33° 59'S, 25° 40'E)	other	190
22.	PEM1073	12 Sep 84	Oyster Bay (34° 10'S, 24° 39'E)	stranding	133
23.	PEM1143	11 Mar 85	7 km E of Swarkops River Mouth	stranding	208
24.	PEM1214	28 Aug 85	Cape Recife, PE (34° 02'S, 25° 42'E)	stranding	165
25.	PEM1453	30 Jan 88	3 km E Kabeljous River Mouth, Jeffreys Bay	stranding	193
26.	PEM1507	5 Feb 88	King's Beach, PE (33° 58'S, 25° 39'E)	stranding	198
27.	PEM1587	18 May 89	Amsterdamhoek (33° 52'S, 25° 38'E)	stranding	192
28.	PEM1706	12 July 90	1.5 km E of Sundays River Mouth, WC	stranding	126
29.	PEM1868	24 Sep 91	Cape Recife, PE (34° 02'S, 25° 42'E), near lighthouse	stranding	199
30.	PEM1882	6 May 92	King's Beach, PE (33° 58'S, 25° 39'E)	stranding	180
31.	PEM1890	13 July 92	Cape Recife, PE (34° 02'S, 25° 42'E)	stranding	192
32.	PEM1891	18 July 92	Hobie Beach, PE (33° 58'50"S, 25° 39' 30"E)	rehab. (D)	137
33.	PEM1892	27 July 92	Sardinia Bay (34° 02'S, 25° 29'E), 800 m E of boat shed	stranding	185
34.	PEM1895	29 July 92	Cape Recife, PE (34° 02'S, 25° 42'E), 2 km E of lighthouse	stranding	188
35.	PEM1900	July 92	NR	rehab. (D)	92
36.	PEM1901	July 92	Jefferys Bay (34° 03' S, 24° 55'E)	rehab. (D)	84
37.	PEM1999	20 July 92	EC trawl grounds (34° 52'S, 23° 35'E–34° 50'S, 23° 48'E)	by-catch	–
38.	PEM2000	21 July 92	EC trawl grounds (34° 50'S, 23° 48'E–34° 48'S, 24° 00'E)	by-catch	–
39.	PEM2001	21 July 92	EC trawl grounds (34° 50'S, 23° 48'E–34° 48'S, 24° 00'E)	by-catch	–
40.	PEM2002	22 July 92	EC trawl grounds (34° 55'S, 23° 14'E–34° 53'S, 23° 26'E)	by-catch	–
41.	PEM2003	24 July 92	EC trawl grounds (34° 51'S, 23° 42'E–34° 49'S, 23° 53'E)	by-catch	–
42.	PEM2004	25 July 92	EC trawl grounds (34° 45'S, 24° 18'E–34° 48'S, 24° 00'E)	by-catch	–
43.	PEM2005	11 Aug 92	EC trawl grounds (34° 43'S, 24° 34'E–34° 40'S, 24° 45'E)	by-catch	–
44.	PEM2006	13 Aug 92	EC trawl grounds 34° 45'S, 24° 25'E–34° 42'S, 24° 40'E)	by-catch	–
45.	PEM2007	14 Aug 92	EC trawl grounds (34° 42'S, 24° 51'E–34° 42'S, 24° 42'E)	by-catch	–
46.	PEM2008	14 Aug 92	EC trawl grounds (34° 41'S, 24° 42'E–34° 38'S, 24° 54'E)	by-catch	–
47.	PEM2009	22 Aug 92	EC trawl grounds (34° 41'S, 24° 45'E–34° 37'S, 24° 59'E)	by-catch	–
48.	PEM2010	22 Aug 92	EC trawl grounds (34° 47'S, 24° 11'E–34° 46'S, 24° 25'E)	by-catch	–
49.	PEM2011	8 Sep 92	EC trawl grounds (33° 50'S, 27° 06'E–34° 37'S, 24° 59'E)	by-catch	–
50.	PEM2014	25 Sep 92	EC trawl grounds (34° 23'S, 26° 04'E–34° 23'S, 25° 58'E)	by-catch	–
51.	PEM2018	25 Jan 93	Bird Island, AB (33° 51'S, 26° 17'E)	stranding	155
52.	PEM2020	28 Jan 93	Kenton-On-Sea (33° 40'S, 26° 40'E)	euthanased	66
53.	PEM2024	30 Jan 93	Woody Cape, AB (33° 46'S, 26° 19'E)	euthanased	74
54.	PEM2035	11 Mar 93	The Pipes, SE of Pollock Beach (33° 59'20"S, 25° 40' 30"E)	stranding	118
55.	PEM2044	28 May 93	Seaview (34° 01'S, 25° 17'E), Otter Pools	stranding	206
56.	PEM2045	30 May 93	Schoenmakerskop (34° 02'S, 25° 32'E)	stranding	145
57.	PEM2046	19 May 93	EC trawl grounds (35° 09'S, 21° 28'E)	by-catch	141
58.	PEM2047	20 May 93	EC trawl grounds (34° 53'S, 23° 27'E–34° 50'S, 23° 40'E)	by-catch	167

continued on next page

continued from previous page

	ID No.	Date of collection	Approximate location[b]	Method of collection[c]	SBL (cm)
59.	PEM2048	20 May 93	EC trawl grounds (34° 53'S, 23° 27'E–34° 50'S, 23° 40'E)	by-catch	157
60.	PEM2049	7 June 93	Kini Bay (34° 01'S, 25° 26'E), Western Beach	stranding	174
61.	PEM2051	28 June 93	EC trawl grounds (34° 44'S, 24° 29'E–34° 45'S, 24° 20'E)	by-catch	168
62.	PEM2052	28 June 93	EC trawl grounds (34° 44'S, 24° 29'E–34° 45'S, 24° 20'E)	by-catch	171
63.	PEM2053	28 June 93	EC trawl grounds (34° 46'S, 24° 21'E–34° 44'S, 24° 32'E)	by-catch	153
64.	PEM2054	29 June 93	EC trawl grounds (34° 45'S, 24° 28'E–34° 47'S, 24° 18'E)	by-catch	165
65.	PEM2055	29 June 93	EC trawl grounds (34° 46'S, 24° 22'E–34° 44'S, 24° 32'E)	by-catch	179
66.	PEM2056	29 June 93	EC trawl grounds (34° 46'S, 24° 22'E–34° 44'S, 24° 32'E)	by-catch	139
67.	PEM2057	30 June 93	Pollock Beach, PE (33° 59'20"S, 25° 40'30"E)	rehab. (D)	172
68.	PEM2081	19 July 93	Cape Recife, PE (34° 02'S, 25° 42'E)	stranding	162
69.	PEM2082	July 93	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	176
70.	PEM2087	17 Aug 93	Plettenberg Bay (34° 07'S, 23° 25'E), Robberg	stranding	190
71.	PEM2131	13 Dec 93	Sundays River Mouth, AB	rehab. (D)	67
72.	PEM2134	28 Dec 93	Noordhoek (34° 02'S, 25° 39'E)	stranding	216
73.	PEM2137	5 Jan 94	Summerstrand, PE (34° 00'S, 25° 42'E)	rehab. (D)	118
74.	PEM2140	17 Jan 94	40 km E of Sundays River Mouth, WC	stranding	187
75.	PEM2141	17 Jan 94	39 km E of Sundays River Mouth, WC	stranding	198
76.	PEM2155	11 Feb 94	10 km E of Sundays River Mouth, WC	stranding	184
77.	PEM2186	7 Apr 94	Amsterdamhoek (33° 52'S, 25° 38'E)	rehab. (D)	90
78.	PEM2188	17 Apr 94	NR	oceanarium	132
79.	PEM2191	4 May 94	Port Alfred (33° 36'S, 26° 55'E)	euthanased	100
80.	PEM2194	2 June 94	Schoenmakerskop (34° 02'S, 25° 32'E)	stranding	194
81.	PEM2198	July 94	Plettenberg Bay (34° 03'S, 23° 24'E)	stranding	105
82.	PEM2203	18 July 94	Port Elizabeth Harbour (33° 58'S, 25° 37'E)	other	204
83.	PEM2238[d]	1994	Durban (29° 50'S, 31° 00'E)	rehab. (D)	96
84.	PEM2248	12 Aug 94	Seaview (34° 01'S, 25° 27'E)	stranding	158
85.	PEM2252	22 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	172
86.	PEM2253	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	152
87.	PEM2254	27 Aug 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	146
88.	PEM2256	17 Sep 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	198
89.	PEM2257B	8 Oct 94	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	170
90.	PEM2348	14 Nov 94	Humewood, PE (33° 59'S, 25° 40'E)	stranding	189
91.	PEM2359	21 Feb 95	Sundays River Mouth, AB	stranding	108
92.	PEM2374	24 Mar 95	Jeffreys Bay (34° 03'S, 24° 55'E)	stranding	186
93.	PEM2379	12 Apr 95	Bokness (33° 41'S, 26° 31'E)	stranding	189
94.	PEM2400	13 July 95	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	176
95.	PEM2403	July 95	NR	rehab. (D)	88
96.	PEM2404	July 95	NR	rehab. (D)	92
97.	PEM2405	July 95	NR	rehab. (D)	87
98.	PEM2406	July 95	Swartkops River Mouth	stranding	154
99.	PEM2411	24 Aug 95	Plettenberg Bay (34° 03'S, 23° 24'E)	by-catch	155
100.	PEM2414	25 Aug 95	EC trawl grounds (c. 30 nm S of Cape St. Francis)	by-catch	148
101.	PEM2415	27 Aug 95	Sardinia Bay (34° 02'S, 25° 29'E)	stranding	130
102.	PEM2454	8 Nov 95	Noordhoek (34° 02'S, 25° 39'E)	stranding	196
103.	PEM2458	3 Dec 95	Cape St. Francis (34° 12'S, 24° 52'E)	rehab. (D)	110

[a] Animal collected in 1980 and issued with a new identification number in 1983, i.e., PEM952.

[b] Kabeljous River Mouth (34° 00'S, 24° 56'E); Maitland River Mouth (33° 59'S, 25° 18'E); Sundays River Mouth (33° 43'S, 25° 51'E); and Van Starden's River Mouth (33° 58'S, 25° 13'E).

[c] Stranding, animal washed up dead on beach (*n* = 47). By-catch, animal incidentally caught in a commercial trawl net during fishing operations (*n* = 32). Rehab. (D), animal died during rehabilitation at the Port Elizabeth Oceanarium (*n* = 13). Euthanased, animal suffering from illness/injury and was put down to prevent further suffering (*n* = 3). Sci. permit, animal collected under scientific permit (*n* = 4). Oceanarium, captive animal of the Port Elizabeth Oceanarium (*n* = 2, PEM676, Tommy; PEM2188, Rascal). Other, animal died from other causes (*n* = 2, PEM958 found floating in the ocean off Humewood Beach; PEM2203 stoned to death by fisherman).

[d] Animal PEM2238 collected NE of the Eastern Cape, i.e., Durban (29° 50'S, 31° 00'E).

NR, not recorded.