

## Morphology, age and survival of adult male New Zealand fur seals, *Arctocephalus forsteri*, in South Australia

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### Abstract

Nineteen adult male New Zealand fur seals, *Arctocephalus forsteri*, were marked and measured at the start of the breeding seasons in November 1992 and 1993 at Cape Gantheaume, Kangaroo Island in South Australia. The age of each seal was estimated from the number of cementum layers in a post-canine tooth. The males that were attempting to hold territories were 7–15 years old and the heaviest was 160 kg. The mass of males could be predicted accurately from linear measurements and several predictive equations enable estimation of mass in the field. The mean annual survival rate for adult male New Zealand fur seals was 76%, which is higher than that in other fur seal species, perhaps reflecting the expanding nature of the *A. forsteri* population in Australia.

### Introduction

Morphological data are a basic requirement for many aspects of biological studies, and there is often a strong relationship between morphology, age and survival. Hence, information on age and morphology can be useful in estimating parameters such as population size and age structure (e.g. Payne 1978). It is particularly important to model these parameters as accurately as possible in marine mammal populations because measures of individuals from the entire population are usually impossible to obtain (Barlow and Boveng 1991). In addition to modelling population parameters, data on morphology and age are required for studies of processes within populations, because age or size can have significant effects on reproduction, foraging ability or movement (e.g. Lunn and Boyd 1993a, 1993b; Modig 1996).

Despite the obvious importance of these characteristics in biological studies, data on the morphology, age and survival of fur seals appear to be scarce, particularly those data relating to territorial adult males. This scarcity has both an historical and, more recently, an ethical basis. Interest in taxonomy and ecology, and hence the need for morphological studies, developed only after the seal populations had been severely depleted by the activities of sealers. Therefore, very few fur seal specimens were available to provide morphological information. Ironically, while fur seal stocks are now at the highest levels since the cessation of sealing, there are now ethical restrictions on killing specimens for scientific studies. Obtaining measurements from live animals can be arduous due to the difficulties of handling such large, aggressive animals.

Although data on the mass, morphology and age of adult male New Zealand fur seals, *A. forsteri*, have been published previously, they have either been based on small sample sizes (e.g. Miller 1975; Mattlin 1978) or appear to be estimates (e.g. Crawley and Wilson 1976). Nevertheless, they have been accorded credence in the literature due to the lack of better data.

Estimating the mass of animals is important for modelling biomass, interpreting physiological and ecological parameters and for techniques such as anaesthesia (Pemberton *et al.* 1993). Mass is particularly difficult to measure in adult male fur seals, the largest members of

any fur seal species, because of the problems of restraining individuals and the difficulties of transporting large balances. Linear measurements can be more easily obtained from restrained animals, or by using indirect methods such as photogrammetry or measuring resting places (e.g. Gallo-Reynoso and Figueroa-Carranza 1996). A predictive relationship between mass and linear measurements would therefore enable field estimation of mass. This has been developed for phocid seals (e.g. Castellini and Kooyman 1990) using a volume index, where the equation is based on the assumption that the shape of the seal is effectively two cones that join at the axilla. Similar predictive equations have been demonstrated in three otariid species, the Steller sea lion, *Eumetopias jubatus* (Castellini and Calkins 1993), the Australian fur seal, *Arctocephalus pusillus doriferus* (Pemberton *et al.* 1993) and the Antarctic fur seal, *A. gazella* (Payne 1979). In the first two studies the measurements were made of adult male seals at various times of the year including the breeding season. Size and shape fluctuate widely in adult male fur seals throughout the year, and it is therefore desirable to determine whether mass can be predicted from linear measurements at the start of the breeding season, when the sizes of adult males are at their annual peak.

The aim of this study was to determine the morphology, age and survival rates of territorial male New Zealand fur seals, and to investigate the relationships between their linear measurements and their mass

## Methods

### *Study site*

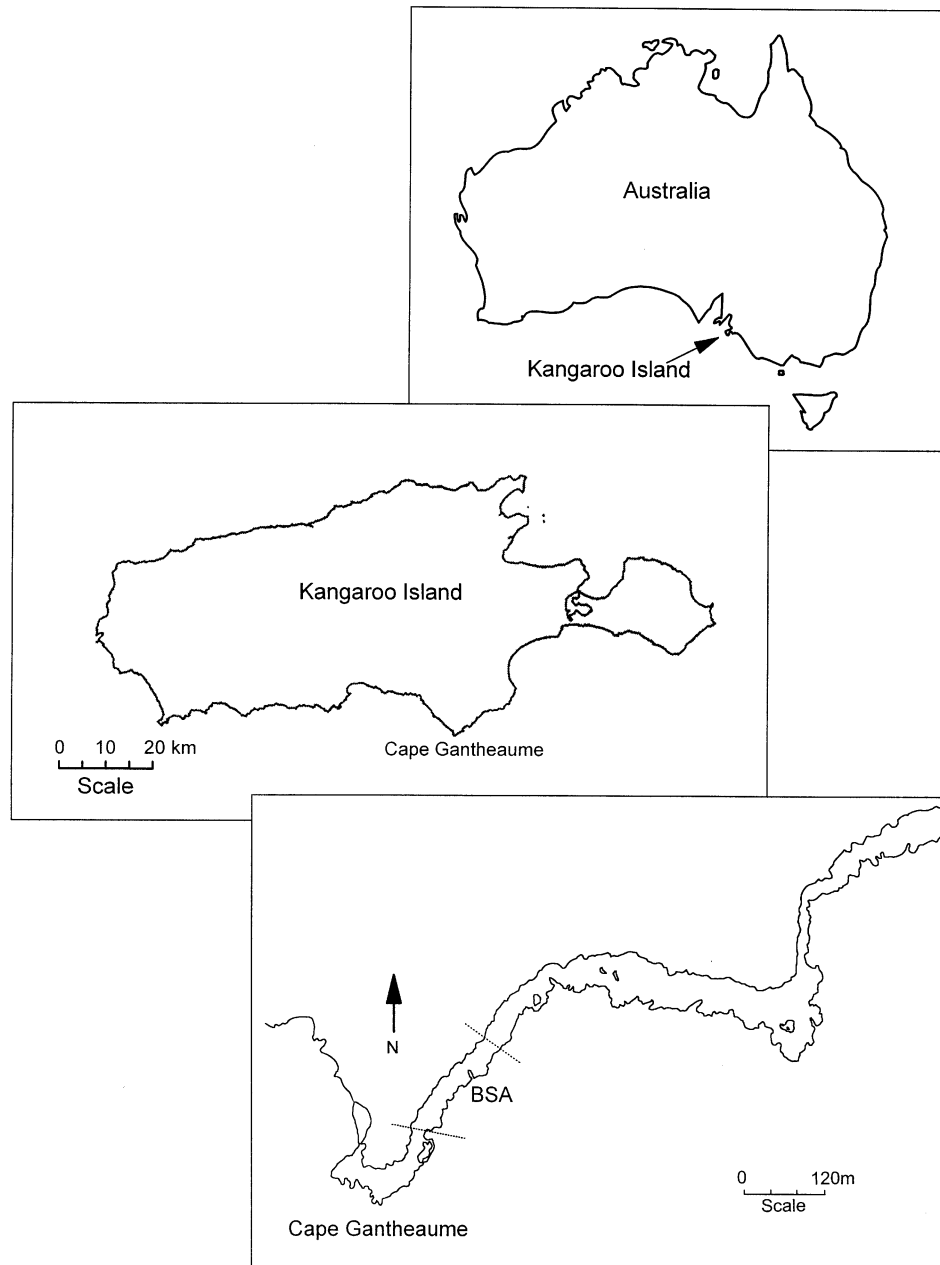
The study took place at the *Arctocephalus forsteri* breeding colony at Cape Gantheaume (36°04'S, 137°28'E), in the Cape Gantheaume Conservation Park on Kangaroo Island in South Australia (Fig. 1). Cape Gantheaume is the southernmost point of Kangaroo Island, and has an irregular rocky platform of Kanmantoo schist skirting the shore. The fur seals haul-out on the rocky platform and the colony currently extends for approximately 1.5 km north-east from the Cape, with most of the seals found towards the southern end. Some 1115 pups were estimated to have been born at the Cape Gantheaume breeding colony in the 1994/95 breeding season and the annual rate of growth of the colony was approximately 16% (Shaughnessy *et al.* 1995).

### *Breeding study area*

The breeding study area (BSA) is situated in the main part of the breeding colony, and was 50 m north-east of the southern point of Cape Gantheaume. The BSA is a section of the rock platform that has approximately 100 m of shoreline. It is bounded on the south-western side by an easily distinguished boundary from the seals breeding immediately to the south, and on the north-eastern side there is a section of flat terrain where few seals breed or haul-out (Fig. 1).

### *Capture*

The breeding season was defined as beginning on the date that the first pup was born (typically November 30) and ending on January 15. This latter date was set because estimates of pup abundance using mark-recapture techniques began at this date each year and many bulls left their territories during the resulting disturbance to the colony. At Cape Gantheaume, 95% of pups are born by January 9 (Shaughnessy, unpublished data); therefore, given the 7-day interval between parturition and oestrus (Goldsworthy and Shaughnessy 1994), 95% of matings with females in oestrus should have occurred by January 16. The adult males that were selected for marking were in the BSA in the weeks preceding the birth of the first pup in November 1992 and November 1993. Males were captured with hand-held hoop nets and anaesthetised for marking (Troy *et al.* 1997). In 1992, 11 males were marked between 18 and 30 November, and in 1993 a further eight males were marked between 27 November and 2 December. In addition, three seals that were marked in November 1992 were recaptured, marked and measured again in November 1993. Adult males were present in the breeding colony at Cape Gantheaume



**Fig. 1.** The breeding study area (BSA) at Cape Gantheaume, Kangaroo Island, South Australia. Insets show the location within Kangaroo Island, and within Australia.

throughout the year although it was difficult to make a distinction between territorial and non-territorial males at the time of marking. For the purposes of this study, a distinction was made between adult male seals and territorial male seals: the former included all the males that were

captured and measured, and the latter referred only to those marked adult male seals that held a territory in the breeding section of the colony during the breeding season following the birth of the first pup.

#### *Marking and measurements*

Once the male was sedated, it was marked with either a freeze-brand on the shoulder (in 1992) or with a hot-iron brand on the flank (in 1993). Animals were tagged with a single white Dalton Jumbo Rototag™ in one foreflipper, and with a circular tag with a radio-transmitter mounted on it on the other foreflipper. The exceptions to this were one male that was double tagged in November 1992, and another male that was recaptured in November 1993, and both the Dalton tag and radio-tag were replaced with two fresh Dalton Rototags. The Dalton tags were embossed with a unique alphanumeric for identification.

Each male was placed on a ladder or stretcher and weighed with a brass clock-face 500-lb scale suspended from a tripod. Masses were recorded to the nearest pound and converted to kilograms (factor = 0.4356). Standard length, curvilinear length and axillary girth (Bonner and Laws 1993) were measured with a flexible measuring tape. The tape was attached to a straight pole for measuring standard length. The body condition index (BCI) of captured adult male seals was calculated as the mass/length ratio:  $BCI = M/L$ , where  $M$  = mass (kg) and  $L$  = standard length (cm) (Arnould 1995). The volume index (VI) was calculated as  $VI = LG^2/10^5$ , where  $L$  = standard length (cm) and  $G$  = axillary girth (cm) (Castellini and Kooyman 1990).

A first post-canine tooth was extracted from each seal so that the age of the animal could be estimated from the cementum layers (see below). In 1992, the first upper left post-canine was extracted but this procedure proved very difficult and it sometimes took more than 10 min to extract a single tooth. In 1993, the first lower left post-canine was extracted; this was found to be much easier, with extraction times of less than 3 min.

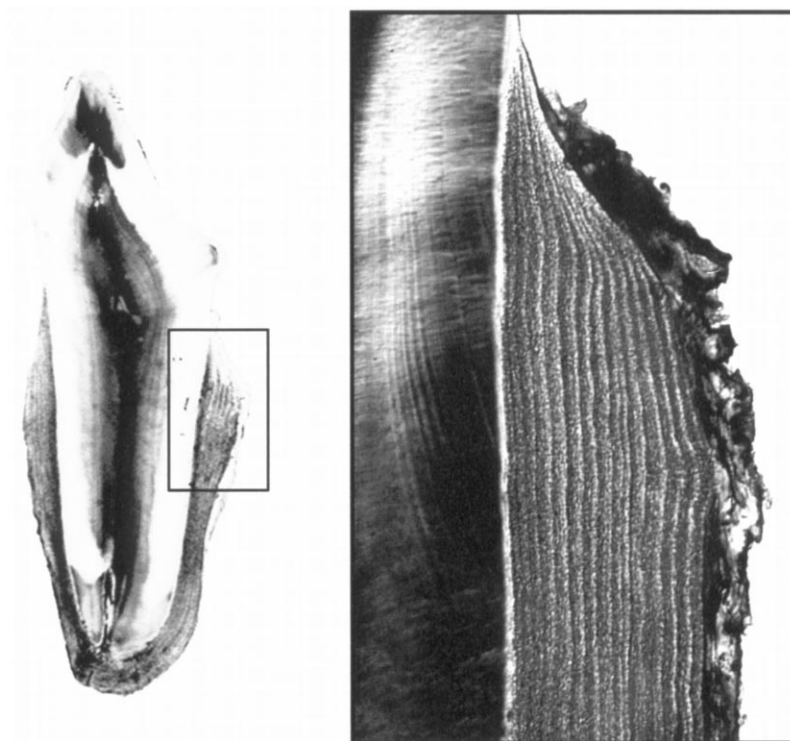
#### *Age estimation*

In 1993, the teeth extracted from the males in the previous breeding season were mounted in glue on a wooden block and sectioned longitudinally using a Buehler Isomet low-speed saw with a 0.4-mm diamond wafering blade. The sections were ground on fine emery paper on a Buehler Ecomet III polisher to eliminate scurf marks from the saw. The sections were approximately 30 µm thick. In 1994, the teeth extracted from male seals in the previous breeding season were mounted in dental wax on a wooden peg and sectioned longitudinally using a horizontal Leitz 1600 Sawing Microtome with a 300-µm diamond blade. At least two longitudinal sections (Fig. 2a) were cut from the midline of each tooth. Sections were stored in 70% ethanol.

The sections were separated and placed in numbered vials, and an age estimate made for each section during 'blind' trials with two readers. The teeth sections were viewed with a polarising filter under a dissecting microscope at 2.5× magnification with a 2× objective lens, and the number of cementum growth layer groups (Fig. 2b) was counted in at least two distinct areas of each section. When sections were viewed under a microscope, the addition of a few drops of 70% alcohol often made growth layer groups easier to distinguish. Each section was presented to the reader at least twice and the maximum number of growth layer groups counted for each tooth was recorded as the final age estimate for each reader. The maximum age recorded from either of the readers was taken as the final age estimate for each seal. The age of each male was assumed to be an integer, because all males would have been caught close to the anniversary of their birth.

#### *Survival*

Daily searches were made throughout the colony during all field trips (Table 1) to locate and identify marked males. Males were recorded as territorial if they were within a breeding area of the colony and in close proximity to adult female fur seals and/or pups.



**Fig. 2.** Longitudinal section through a post-canine tooth of an adult male *Arctocephalus forsteri*. Inset shows detail of growth layer groups in the cementum layer, which is on the right side.

**Table 1.** Dates and duration of field trips to the fur seal colony at Cape Gantheaume, during which daily searches were made for marked adult male *Arctocephalus forsteri*

Season	Year	Dates of field trips
Breeding	1992/93	15 November 1992 – 24 January 1993
Non-breeding	1993	16–24 May, 20 July – 7 August 1993
Breeding	1993/94	15 November 1993 – 8 February 1994
Non-breeding	1994	16 May – 12 June, 8–31 August 1994
Breeding	1994/95	14 November 1994 – 27 January 1995
Breeding	1995/96	9–10 December 1995, 2 & 10–14 January 1996
Breeding	1996/97	7–8 December 1996, 2 January 1997
Breeding	1997/98	19–22 December 1997, 2 January 1998

## Results

### *Mass, morphology, age and survival*

The mean mass of all adult male seals that were captured was  $126.3 \pm 22.9$  (s.d.) kg (Table 2), with a maximum of 160 kg in 1992 and 148 kg in 1993. The mass of the males was significantly correlated with the date of capture (i.e. larger males were caught later in the season). This was the case in 1992, when both the mass and body condition (BCI) of all males

**Table 2. Morphological measurements of adult male *Arctocephalus forsteri* at Cape Gantheaume**

$n$  = sample size; values in parentheses refer to sample sizes for the axillary girth data, where one of the captured animals was not measured. Comments indicate the territorial status of the individuals (see Methods in text). 'Excl. recaptures' indicates that the three males that were recaptured in 1993 were excluded from the sample

Year	$n$ (kg)	Mass length (cm)		Standard length (cm)		Curvilinear (cm)		Axillary girth Comments		
		Mean	s.d.	Mean	s.d.	Mean	s.d.	Mean	s.d.	
1992	8	137.6	15.7	168.8	6.2	177.3	8.3	134.7	5.9	territorial only
1992	11	126.6	24.2	166.3	8.1	173.9	9.9	128.3	13.1	all males captured
1993	9 (8)	136.1	14.7	167.8	5.1	174.2	4.7	129.0	11.0	territorial only
1993	11 (10)	129.1	20.8	166.7	5.2	172.7	5.4	125.7	12.0	all males incl. recaptures
1993	6	135.6	15.9	167.7	6.0	173.4	5.7	130.6	12.2	territorial excl. recaptures
1993	8	126.0	22.6	166.2	5.8	171.6	6.0	126.0	13.4	all males excl. recaptures
Both	19	126.3	22.9	166.2	7.0	172.9	8.4	127.3	12.9	all males excl. recaptures

**Table 3. Correlations of mass or condition with the date of capture for adult male *Arctocephalus forsteri* at Cape Gantheaume in November 1992 and November 1993**

'Excl. recaps' indicates that animals that had been captured and measured previously were excluded from the calculation

Year	Variable	Pearson's $r$	$n$	$P$
1992 and 1993	mass (kg)	0.576	22	0.005
1992	mass (kg)	0.737	11	0.010
1992	condition	0.739	11	0.010
1993	mass (kg)	0.332	11	0.319
1993	condition	0.409	11	0.212
1993 (excl. recaps)	mass (kg)	0.159	8	0.707
1993 (excl. recaps)	condition	0.215	8	0.611

were significantly correlated with the date of capture, but not in 1993, when neither mass nor BCI was significantly correlated with capture date (Table 3).

The mean values for standard length, curvilinear length and axillary girth for all of the captured males and the subset of territorial males are given in Table 2. The maximum standard length, curvilinear length and axillary girth were 179 cm, 188 cm, and 142 cm respectively.

The range of BCI of the adult male seals was 0.52–0.94, and the mean was 0.76. The mean BCI was not significantly different between years (pooled variances  $t = 0.04$ , d.f. = 17,  $P = 0.97$  excluding recaptured animals).

The ages of the seals estimated by the two readers were highly correlated ( $r = 0.95$ ,  $P < 0.01$ ) but in the 47% of cases where the readers disagreed, one reader estimated older ages in the majority of cases (paired sample t-test, mean difference = 0.37, s.d. difference = 0.76,  $t = 2.11$ , d.f. = 18,  $P = 0.05$ ).

The estimated age range of adult male seals was 7–15 years. The mean estimated age at first capture for all marked adult males was 10.7. In 1992, the mean estimated age for territorial males was 10.4 years and in 1993 it was 12.0 years (Table 4). The estimated age of territorial males was not significantly different between years (separate variances  $t = 1.68$ , d.f. = 11.8,  $P = 0.12$ ).

The mean annual survival was 0.76 (95% CI = 0.66–0.82), estimated using a Kaplan–Meier estimate of survival (Pollock *et al.* 1989) based on the number of years animals were known to be alive after they were marked. This method interprets survival as the cumulative probability of a marked animal surviving and being present in the breeding colony after time (years) (Table 5). This is the minimum approximation of survival, since it is based on the number of animals known to be alive; the animals could have gone somewhere else or lost their marks. The mean annual survival of marked males over the five years of the study was calculated as the fifth root of the cumulative survival.

The minimum rate of tag loss was calculated by including only the animals known to have lost their tag; whereas the maximum loss rate was calculated by also including the animals that were not sighted with those that were known to have lost their tag. The annual rate of tag loss varied between years and increased with the amount of time a male wore a tag. After 12 months, 0–18% of males had lost a tag, 11–39% lost a tag after 24 months, and 30–70% had lost a tag after 36 months.

#### *Relationship between morphology and age*

There was a significant positive relationship between age and mass in adult males in this study ( $r = 0.44$ ,  $P = 0.03$ ) and the regression equation of mass on age was

$$\text{Mass (kg)} = 80.030 + 4.332 \times \text{age (in years)}.$$

**Table 4. Ages of adult male fur seals captured at the start of the 1992 and 1993 breeding seasons at Cape Gantheaume**

‘Comments’ indicates the territorial status of captured males (see Methods in text). ‘Excl. recaps’ indicates that the three males that were recaptured in 1993 were excluded from the sample

Year	Median	Mode	Mean	s.d.	<i>n</i>	Comments
1992	11	8	10.4	2.4	8	Territorial
1992	11	11	10.1	2.3	11	All males
1993	12	14	12.0	2.2	9	Territorial
1993	11	14	11.5	2.3	11	All males
1993	12	11	12.3	2.0	6	Territorial excl. recaps
1993	11	11	11.5	2.3	8	All males excl. recaps
Both	11	11	10.7	2.3	19	All males excl. recaps

**Table 5. Kaplan–Meier estimates of cumulative survival for marked adult male fur seals, modified to allow for the staggered entry of new animals into the study (after Pollock *et al.* 1989)**

‘No. at risk’ = number of animals known to be alive at the start of the period; ‘no. deaths’ = number of animals known to have died during the period; ‘no. censored’ = number of animals not seen during the period hence not known to be alive; and ‘no. new added’ = number of new animals marked during the period. Cumulative survival is the cumulative probability of a marked male surviving and being sighted within the colony after time (years)

Time (years)	Dates	No. at risk	No. deaths	No. censored	No. new added	Cumulative survival	Lower 95% CI bound	Upper 95% CI bound
0	15 Nov. 1992 – 14 May 1993	11	0	0	0	1.000	1.000	1.000
1	15 Nov. 1993 – 14 May 1994	11	1	0	8	0.909	0.747	1.071
1.5	15 May 1994 – 14 Nov. 1994	18	0	2	0	0.808	0.645	0.972
2	15 Nov. 1994 – 14 Nov. 1995	16	0	2	0	0.707	0.520	0.895
3	15 Nov. 1995 – 14 Nov. 1996	14	0	0	0	0.737	0.539	0.935
4	15 Nov. 1996 – 14 Nov. 1997	14	0	3	0	0.556	0.362	0.750
5	15 Nov. 1997 – 14 Nov. 1998	11	0	6	0	0.253	0.124	0.382

The age of adult males did not correlate with their standard length ( $r = 0.30$ ,  $P = 0.103$ , 27% power to detect an increase of 1 cm per year at  $\alpha = 0.05$ ), nor did the age of territorial males correlate with their standard length ( $r = 0.15$ ,  $P = 0.30$ ).

#### *Predictive relationships for mass from linear measurements*

The predictive equations and statistics for the relationships between mass and linear measurements are summarised in Table 6. There was a significant regression of mass on volume index [ $\text{LG}^2/10^5$ ] (Fig. 3a). The regression equation for the mass on volume index was also forced through the origin, which also led to a significant relationship.

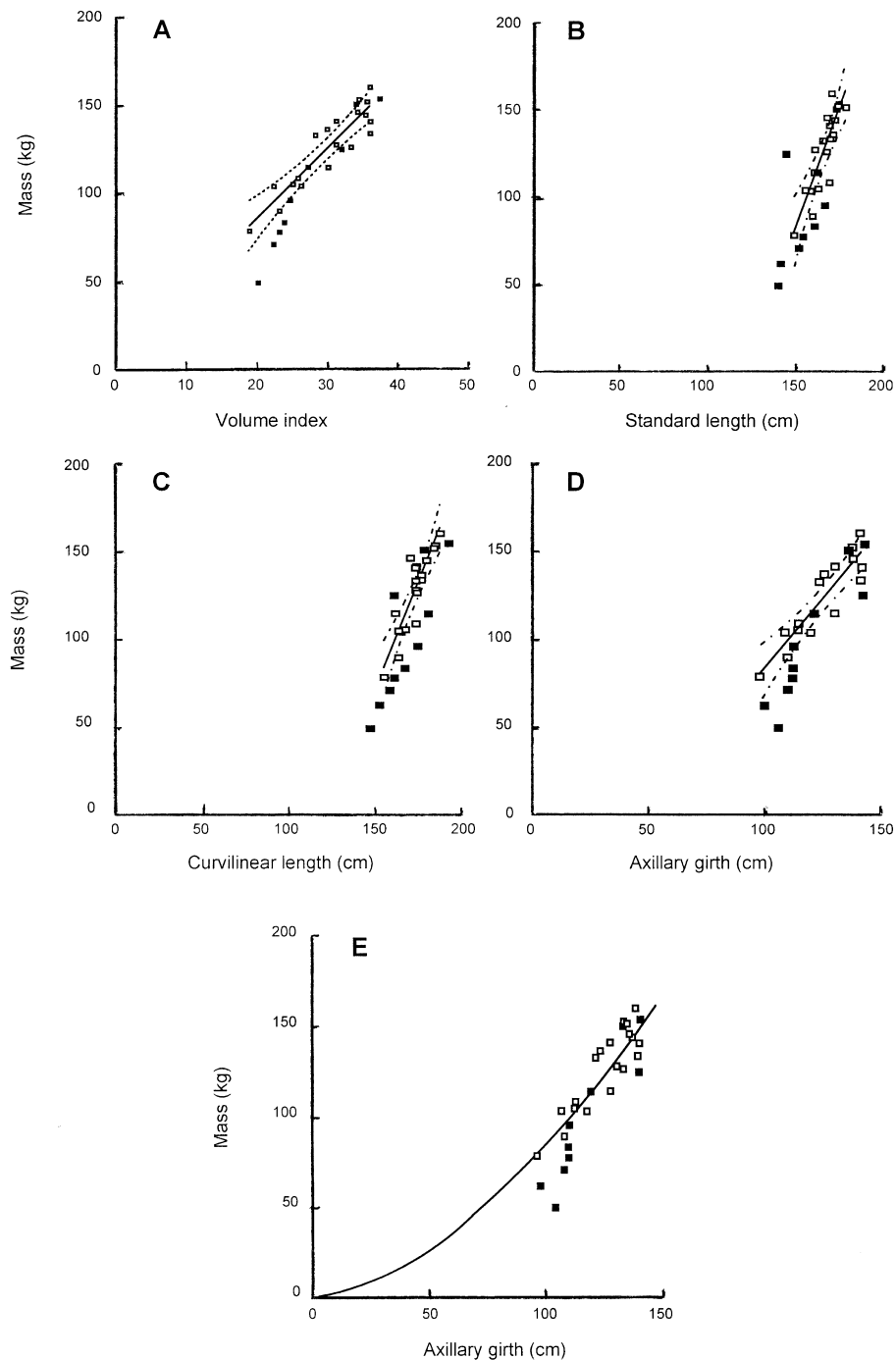
There were also significant regressions of mass on standard length (Fig. 3b), curvilinear length (Fig. 3c), and axillary girth (Fig. 3d). A curvilinear function was also used to predict mass

**Table 6. Equations from regressions of mass with morphological measurements on adult male fur seals from South Australia (this study) and from New Zealand (Mattlin 1978)**

All mass measurements are in kilograms; linear measurements are in centimetres. See text for explanation of volume index,  $10^{-5}$  [ $\text{LG}^2$ ].  $P$  indicates the probability that the slope of the regression equation is not significantly different from zero.  $r^2$  indicates the proportion of the variation in mass that is explained by the regression equation. ‘Mattlin’ indicates regression equations that included the data from this study and those of Mattlin (1978). All regression equations included a constant unless otherwise indicated

Regression	Equation	$r^2$	$n$	$P$	Comments
Mass on ...	Mass =				
Volume index	$31.029 + 3.482 \times 10^{-5} [\text{LG}^2]$	0.844	19	0.0005	linear
Volume index	$4.566 \times 10^{-5} [\text{LG}^2]$	0.993	19	0.0005	linear, forced through origin
Std length	$-333.593 + 2.767 \times (\text{std length})$	0.719	19	0.0005	linear
Curv length	$-297.545 + 2.451 \times (\text{curv length})$	0.800	19	0.0005	linear
Axillary girth	$-75.685 + 1.587 \times (\text{axillary girth})$	0.799	19	0.0005	linear
Axillary girth	$0.036 \times (\text{axillary girth})^{1.68}$	0.829	19	0.0005	curvilinear function
Std length	$-297.736 + 2.541 \times (\text{std length})$	0.689	29	0.0005	Mattlin
Volume index	$4.801 + 4.327 \times 10^{-5} [\text{LG}^2]$	0.876	29	0.0005	Mattlin, forced
Volume index	$4.502 \times 10^{-5} [\text{LG}^2]$				through origin





**Fig. 3.** The relationship between mass and linear measurements of adult male *Arctocephalus forsteri*. The linear regression lines refer only to individuals from this study, with 95% confidence limits and show (A) mass against volume index (see text); (B) mass against standard length; (C) mass against curvilinear length; (D) mass against axillary girth. (E) illustrates the curvilinear relationship  $\text{Mass} = 0.036 \times (\text{axillary girth})^{1.68}$ . Open symbols indicate individuals from this study, closed symbols indicate individuals from Mattlin (1978).

from axillary girth to facilitate comparison with predictions for Antarctic fur seals (Payne 1979); this relationship was also significant (Fig. 3e).

An analysis of covariance was used to compare the results from this study with those of other published measurements of territorial male New Zealand fur seals from New Zealand (Mattlin 1978). There were significant differences between the two studies in the relationship between mass and axillary girth (ANCOVA:  $F_{1,26} = 7.179$ ,  $P = 0.013$ ) and between mass and curvilinear length (ANCOVA:  $F_{1,26} = 7.609$ ,  $P = 0.010$ ), but there were no significant differences between the two studies in the relationship between mass and standard length (ANCOVA:  $F_{1,26} = 0.643$ ,  $P = 0.430$ ). These last data were then pooled to produce a predictive equation for the mass of *A. forsteri* males from standard length (Table 6). There was a significant regression of volume index on mass with the data from this study and that of Mattlin (1978) combined, and the equation from the line forced through the origin was also significant (Table 6).

Although transforming the mass values by taking natural logarithms slightly improved the fit of the data, for ease of calculation in the field, the equations are given for the untransformed data.

## Discussion

### *Mass and linear measurements*

Few studies have reported masses for adult male *A. forsteri*, presumably because of the difficulty in catching and weighing animals in the field. The maximum mass recorded in this study was 160 kg, and this male appeared comparable in size to most territorial males in the colony although some were larger. The mean mass of all the males measured in this study (126.3 kg) is within the range (49.5–154.1 kg) reported for territorial males of this species in New Zealand by Mattlin (1978).

If large size is important for adult males to acquire and maintain territories, size may be a factor in the timing of a male's arrival at the breeding colony. Males that arrive at the colony early, prior to the start of the breeding season, may have an advantage over challengers by having prior residence and greater knowledge of the territory. Conversely, males that arrive later may minimise the use of valuable fat reserves for fasting and maximise the number of potential mates that are available because the number of females ashore increases over the first few weeks of the breeding season. Males may strike a balance between these two strategies. The number of female fur seals at the colony is very low during October and November, and begins to increase rapidly from early December, following the birth of the first pup (Goldsworthy and Shaughnessy 1994; Troy 1997). Males are unlikely to encounter many female seals in oestrous before the birth of the first pup each season, although the timing of oestrous in nulliparous females is unknown in *A. forsteri*. Therefore, males should minimise the time spent holding a territory prior to the start of the breeding season, here defined as the birth of the first pup. One might expect the smaller males to arrive before the larger males because they would have little chance of establishing a territory once the larger males had arrived and established their territories. In this study, larger males were caught closer to the start of the breeding season than smaller males in 1992 but this was not the case in 1993. The absence of a relationship in 1993 may be due to the narrower range of capture dates, because all males in that year were captured within five days, whereas in 1992 the captures were spread over 12 days.

The relationship between male size and arrival at the colony may explain the difference between the mean mass of territorial males of *A. forsteri* in Mattlin's (1978) study and those in this study. The majority of the territorial animals in the former study were shot in October and November, and they may have been smaller than those that held territories during the middle of the breeding season.

Linear measurements of the 19 *A. forsteri* adult males from Kangaroo Island were all similar to the reported range for this species (Miller 1975; Mattlin 1978), and within the range reported for other arctocephaline species (e.g. Croxall and Gentry 1987). Other studies of otariids suggest that the length attained by males at age 7–8 is close to the maximum adult length (*A. gazella*:

Payne 1979; *Otaria flavescens*: Rosas *et al.* 1993). The age range of the male *A. forsteri* in this study was 7–15 years, which suggests that the maximum length of males of this species is unlikely to be much greater than the measurements reported here.

Growth layer groups in the cementum layer of teeth are commonly used to estimate age in pinnipeds, and this method has been validated in a congeneric fur seal species, *A. gazella* (Payne 1978; Arnbom *et al.* 1992). The post-canine teeth of adult male *A. forsteri* showed clear lines in the cementum and most captured adult male *A. forsteri* in this study were 11–12 years of age, with animals older than 7 years attempting to hold territories. These age estimates accord well with those reported by Mattlin (1978), where territorial *A. forsteri* males were 7–15 years of age, and are comparable with those reported for territorial males of other *Arctocephalus* species (e.g. Warneke and Shaughnessy 1985; Bester 1990; Boyd and Roberts 1993), and also with territorial male northern fur seals, *Callorhinus ursinus* (Johnson 1968; Vladimirov 1987). It is not clear whether the small differences in the age ranges of territorial males published for each species reflect real differences in maturation rates or are the result of differences in sampling or in estimating age.

#### *Predictive relationships for mass from linear measurements*

The relationships between mass and size (e.g. length or girth) of territorial male *A. forsteri* are similar to those in other seal species. The relationship between mass and volume index for the males in this study was slightly strengthened with the addition of Mattlin's (1978) data such that 87.6% of the variance in mass was explained by the equation  $\text{Mass (kg)} = 4.801 + 4.327 \times [\text{LG}^2/10^5]$ ; and the equation for the line forced through the origin was  $\text{Mass (kg)} = 4.502 \times [\text{LG}^2/10^5]$ , which explained 99.2% of the variance in mass. The regression coefficient for this latter equation is similar to those published for other seals (Table 7).

Forcing the line through the origin falsely inflates the variance explained by the relationship as it is equivalent to adding an outlier and therefore has great leverage. The equations without constants for *A. forsteri* are given here to facilitate comparison with other published studies but for predictive purposes it is advisable to use the relationships that include a constant.

The strong relationship of mass with the volume index and also with linear measurements, particularly standard length, showed that mass can be accurately predicted using linear measurements at the beginning of the breeding season. This enables field estimates of mass without requiring cumbersome and expensive balances. It is likely that the correlation of mass with standard length would weaken if males were measured throughout the year, due to the large fluctuations in mass and presumably little fluctuation in length in these animals. Conversely, axillary girth is likely to reflect differences in mass throughout the year more accurately. The regression equation of mass on volume index explained the highest proportion of the variation in mass, presumably because it incorporates both length and girth. Therefore, we recommend that this model be used wherever it is impracticable to measure mass directly but both the linear measurements are possible.

#### *Survival*

The minimum mean annual survival rate of adult male *A. forsteri* (76%) tended to be higher than the few published data for survival rates in other fur seal species; the 95% confidence interval for survival (66–82%) overlapped with that for *C. ursinus* but was higher than that for *A. gazella*. The annual survival of adult male *C. ursinus* has been estimated several times, with results between 60 and 67% (Chapman 1964; Peterson 1965; Johnson 1968; Gentry 1997) and in territorial male *A. gazella* it has been estimated at 43% (Arnould and Duck 1997). The estimates of survival from this study were gained from observations of marked males, as were those of Peterson (1965), Gentry (1997) and Arnould and Duck (1997), so the high survival rate in *A. forsteri* is unlikely to be due to the technique of estimation. Potential explanations for the high survival rate of males in this study of *A. forsteri* include the expanding population and biases associated with the capturing technique.

The capturing technique in this study may have produced a bias for selecting the most aggressive males, and perhaps those that were most successful in fights, since most *A. forsteri* males run away from humans. Several other studies were also based on observations of the survival of marked males and thus were also semi-longitudinal studies (Peterson 1965; Gentry 1997). However, the marking techniques of these studies were potentially less biased towards the most aggressive individuals as they did not necessarily rely on capturing the animals to mark them (Gentry 1997), or the animals were captured using more remote methods such as darting them with projectile syringes (Peterson 1965). In addition, *A. gazella* and *C. ursinus* are less inclined to run from humans than are *A. forsteri*, which would allow researchers to sample individuals other than the most aggressive.

Alternatively, the high survival rate of males in this study may be typical of the high general survival rates in an expanding population. Pup production in the fur seal colony at Cape Gantheaume has been increasing at a rate of approximately 16% per annum since population monitoring began in 1988 (Shaughnessy *et al.* 1995) and this increase coincides with an exponential increase in the numbers of adult males in the colony at the height of the breeding season (approximately 19.6% annually; Shaughnessy, unpublished). Pup survival rates for *A. forsteri* at this colony are also high when compared with those published for other fur seal species (Wickens and York 1997). In contrast, the populations of *A. gazella* and *C. ursinus* from which the mortality rates for males were estimated were not expanding.

#### *Relationship between morphology and age*

The positive relationship between total body mass and age of adult male *A. forsteri* is consistent with that in other fur seal species, such as *C. ursinus* and *A. gazella*, where older males are larger (Payne 1979; York 1987). But the relationship explains relatively little of the variance in mass. The mass of male fur seals may vary enormously over the course of the year, so it is not surprising that their masses are quite variable with respect to age. Males probably fluctuate in mass throughout their lives because some of them begin fasting during the breeding season while still subadult or juveniles. Fasting is not confined to territorial males: juvenile and subadult male northern fur seals lose 20–30% of their mass during fasts in the breeding season (Baker *et al.* 1994). It is probable that similar behaviour occurs in *Arctocephalus* species. Although there are no published measurements for mass fluctuations in *A. forsteri*, territorial male *A. gazella* that have similar tenure durations lost 12–42% of their starting mass during the tenure of their territories (analysis of data in Boyd and Duck 1991). The masses of territorial males will depend on their variable history of annual mass changes, particularly their dramatic annual mass changes in recent years. Therefore, it would be surprising if the masses of fur seal males were strongly correlated with their age. On the other hand, one would expect the mass of male fur seals to correlate more strongly with age on a broader scale; that is, when the age range is extended to include subadults and juveniles, as occurs in Antarctic fur seals (Payne 1979) and northern fur seals (York 1987).

In view of the large proportion of mass that fasting fur seal males lose during the breeding season, mass data may be significantly influenced by the duration and timing of data collection, and the degree of synchrony in the timing of male arrival at the breeding colonies. For example, mass data collected from males at the start of the breeding season (when the first pups are born) are likely to have a greater mean than those obtained towards the end of the season, because males later in the season may have lost significant amounts of weight through fasting. This effect may be especially strong if most males arrive at the start of the season and there is little turn-over in territory ownership. Similarly, mass data collected over a period of two weeks may have a significantly different mean than those collected for the same number of individuals in a single day.

Male age was not correlated with standard length in this study, which is consistent with the study of territorial *A. forsteri* males in New Zealand (Mattlin 1978). Analysis of data recorded by Mattlin (1978) revealed that age was not correlated with standard length ( $r = -0.007$ ,  $n = 10$ ,

$P = 0.98$ ). Again, this lack of association between age and body length may be due to the narrow range of ages in territorial males; age would probably correlate with standard length if younger, non-territorial males were included in the sample.

In summary, adult male *A. forsteri* of Cape Gantheaume, Kangaroo Island, South Australia are comparable to those in New Zealand in morphology and age. The body mass of adult males can be predicted from linear measurements, and the survivorship of adult males appears to be higher than those of males of other fur seal species.

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### References

- Ambom, T. A., Lunn, N. J., Boyd, I. L., and Barton, T. (1992). Aging live Antarctic fur seals and southern elephant seals. *Marine Mammal Science* **8**, 37–43.
- Arnould, J. P. Y. (1995). Indices of body condition and body composition in female Antarctic fur seals (*Arctocephalus gazella*). *Marine Mammal Science* **11**, 301–313.
- Arnould, J. P. Y., and Duck, C. D. (1997). The costs and benefits of territorial tenure, and factors affecting mating success, in male Antarctic fur seals. *Journal of Zoology, London* **241**, 649–664.
- Baker, J. D., Fowler, C. W., and Antonelis, G. A. (1994). Mass change in fasting immature male northern fur seals. *Canadian Journal of Zoology* **72**, 326–329.
- Barlow, J., and Boveng, P. (1991). Modeling age-specific mortality for marine mammal populations. *Marine Mammal Science* **7**, 50–56.
- Bester, M. N. (1990). Reproduction in the male sub-Antarctic fur seal *Arctocephalus tropicalis*. *Journal of Zoology, London* **222**, 177–185.
- Bonner, W. N., and Laws, R. M. (1993). Morphometrics, specimen collection and preservation. In 'Antarctic Seals: Research Methods and Techniques'. (Ed. R. M. Laws.) pp. 161–171. (Cambridge University Press: Cambridge, UK.)
- Boyd, I. L., and Roberts, J. P. (1993). Tooth growth in male Antarctic fur seals (*Arctocephalus gazella*) from South Georgia: an indicator of long-term growth history. *Journal of Zoology, London* **229**, 177–190.
- Boyd, I. L., and Duck, C. D. (1991). Mass changes and metabolism in territorial male Antarctic fur seals (*Arctocephalus gazella*). *Physiological Zoology* **64**, 375–392.
- Castellini, M. A., and Calkins, D. G. (1993). Mass estimates using body morphology in Steller sea lions. *Marine Mammal Science* **9**, 48–54.
- Castellini, M. A., and Kooyman, G. L. (1990). Length, girth and mass relationships in Weddell seals (*Leptonychotes weddellii*). *Marine Mammal Science* **6**, 75–77.
- Chapman, D. G. (1964). A critical study of Pribilof fur seal population estimates. *US Fish and Wildlife Service Fisheries Bulletin* **63**, 657–769.
- Crawley, M. C., and Wilson, G. J. (1976). The natural history and behaviour of the New Zealand fur seal (*Arctocephalus forsteri*). *Tuatara* **22**, 1–29.
- Croxall, J. P., and Gentry, R. L. (1987). The 1984 fur seal symposium: an introduction. In 'Status, Biology, and Ecology of Fur Seals. Proceedings of an International Symposium and Workshop'. (Eds J. P. Croxall and R. L. Gentry.) pp. 1–4. NOAA Technical Report NMFS Series 51.

- Gallo-Reynoso, J.-P., and Figueroa-Carranza, A.-L. (1996). Size and weight of Guadalupe fur seals. *Marine Mammal Science* **12**, 318–321.
- Gentry, R. L. (1997). 'Behavior and Ecology of the Northern Fur Seal.' (Princeton University Press: Princeton, USA.)
- Goldsworthy, S. D., and Shaughnessy, P. D. (1994). Breeding biology and haul-out pattern of the New Zealand fur seal, *Arctocephalus forsteri*, at Cape Gantheaume, South Australia. *Wildlife Research* **21**, 365–376.
- Johnson, A. M. (1968). Annual mortality of territorial male fur seals and its management significance. *Journal of Wildlife Management*. **32**, 94–99.
- Lunn, N. J., and Boyd, I. L. (1993a). Effects of maternal age and condition on parturition and the perinatal period of Antarctic fur seals. *Journal of Zoology, London* **229**, 55–67.
- Lunn, N. J., and Boyd, I. L. (1993b). Influence of maternal characteristics and environmental variation on reproduction in Antarctic fur seals. *Symposium of the Zoological Society, London* **66**, 115–129.
- Mattlin, R. H. (1978). Population biology, thermoregulation and site preference of the New Zealand fur seal, *Arctocephalus forsteri* (Lesson, 1828), on the Open Bay Islands, New Zealand. Ph.D. Thesis, University of Canterbury, New Zealand.
- Miller, E. H. (1975). Body and organ measurements of fur seals, *Arctocephalus forsteri* (Lesson), from New Zealand. *Journal of Mammalogy* **56**, 511–513.
- Modig, A. O. (1996). Effects of body size and harem size on male reproductive behaviour in the southern elephant seal. *Animal Behaviour* **51**, 1295–1306.
- Payne, M. R. (1978). Population size and age determination in the Antarctic fur seal *Arctocephalus gazella*. *Mammal Review* **8**, 67–73.
- Payne, M. R. (1979). Growth in the Antarctic fur seal *Arctocephalus gazella*. *Journal of Zoology, London* **187**, 1–20.
- Pemberton, D., Kirkwood, R., Gales, R., and Renouf, D. (1993). Size and shape of male Australian fur seals, *Arctocephalus pusillus doriferus*. *Marine Mammal Science* **9**, 99–103.
- Peterson, R. S. (1965). Behavior of the northern fur seal. D.Sc. Thesis, Johns Hopkins University, Baltimore, USA.
- Pollock, K. H., Winterstein, S. R., Blinch, C. M., and Curtis, P. D. (1989). Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* **53**, 7–15.
- Rosas, R. C. W., Haimovici, M., and Pinedo, M. C. (1993). Age and growth of the South American sea lion *Otaria flavescens* (Shaw) in southern Brazil. *Journal of Mammalogy* **74**, 141–147.
- Shaughnessy, P. D., Goldsworthy, S. D., and Libke, J. A. (1995). Changes in the abundance of New Zealand fur seals, *Arctocephalus forsteri*, on Kangaroo Island, South Australia. *Wildlife Research* **22**, 201–215.
- Troy, S. K. (1997). Territorial behaviour and mating success in male New Zealand fur seals, *Arctocephalus forsteri*. Ph.D. Thesis, University of Melbourne, Australia.
- Troy, S. K., Middleton, D., and Phelan, J. (1997). Capture, anaesthesia and branding of adult male New Zealand fur seals, *Arctocephalus forsteri*. In 'Marine Mammal Research in the Southern Hemisphere'. (Eds M. A. Hindell and C. M. Kemper.) pp 179–183. (Surrey Beatty & Sons: Melbourne, Australia.)
- Vladimirov, V. A. (1987). Age-specific reproductive behavior in northern fur seals on the Commander Islands. In 'Status, Biology, and Ecology of Fur Seals. Proceedings of an International Symposium and Workshop'. (Eds J. P. Croxall and R. L. Gentry.) pp. 113–120. NOAA Technical Report NMFS Series 51.
- Warneke, R. M., and Shaughnessy, P. D. (1985). *Arctocephalus pusillus*, the South African and Australian fur seal: taxonomy, evolution, biogeography, and life history. In 'Studies of Sea Mammals in South Latitudes'. (Eds J. K. Ling and M. M. Bryden.) pp. 53–77. (South Australian Museum: Adelaide.)
- Wickens, P., and York, A. E. (1997). Comparative population dynamics of fur seals. *Marine Mammal Science* **13**, 241–292.
- York, A. E. (1987). Northern fur seal, *Callorhinus ursinus*, Eastern Pacific population (Pribilof Islands, Alaska, and San Miguel Island, California). In 'Status, Biology, and Ecology of Fur Seals'. (Eds J. P. Croxall and R. L. Gentry.) pp. 9–21. NOAA Technical Report NMFS Series 51.