Suture Index as an Indicator of Chronological Age in the Male South African Fur Seal, *Arctocephalus pusillus* (Pinnipedia: Otariidae)

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The South African fur seal (*Arctocephalus pusillus pusillus*) is very closely related to the Australian fur seal (*A. pusillus doriferus*). We examine skull suture index (**SI***) as an indicator of chronological age in the male South African fur seal, based on 42 animals of known age ranging from 10 m to 11 y 11 m. Twenty one (21) animals were aged based upon tagging as pups and 21 were aged based on dentine growth layers (1 to 11 y). Age is approximately directly proportional to suture index [Age = $(0.7990 \pm 0.02354) \times$ **SI***, r = 0.8887, n = 42, valid **SI*** range 0 – 16, useful predictive range 0-≈14 y)]. We describe the sequence of cranial suture closure (n = 11 sutures, 69 animals) and determine whether suture index (**SI***) reliably corresponds to chronological age. Sutures do not close in a definitive order in all individuals and some sutures take longer to close than others. In animals ≤ 12 y, the general sequence of full suture closure was the Basioccipito-basisphenoid, Occipito-parietal, Interparietal, Coronal and finally the Squamosal-jugal. The Maxillary, Squamosal-parietal, Interfrontal, Basisphenoid-presphenoid, Internasal were used in the **SI*** calculation even though none showed any sign of closure in the known-age individuals but did show some closure in very old animals of indeterminate age. Suture closure criteria are useful in classifying males into juveniles, subadults and adults. Multiple linear regression might also prove to be useful to predict chronological age from suture closure data but its utility was limited in the present study by both the size of the data set available and the lack of animals with a known age older than 12y. More data is needed on old animals of known age but the relationship between skull sutures and age found in the present study would be sufficient for aging most male skull material because very few males are likely to reach ages greater than about 12-14 y.

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INTRODUCTION

Age determination in pinnipeds is important in many studies of their biology and ecology, particularly those examining development and growth. Various techniques have been used to determine absolute or at least relative age in pinnipeds. Techniques include: examination of tooth structure, the use of incremental structures in nails and bones, suture closure, standard body length, baculum development, eye lens weight, ovarian structure, and pelage characteristics (see Laws 1962; Jonsgard 1969; Morris 1972; McCann 1993; McLaren 1993). Currently, examination of tooth structure is the most precise method of age determination in pinnipeds (Scheffer 1950; Laws 1953; McCann 1993; McLaren 1993) and has been used to successfully age the South African fur seal (*Arctocephalus pusillus pusillus*) (Fletemeyer 1978;

Oosthuizen 1997; Stewardson et al. 1998; Stewardson 2001; Stewardson et al. 2008). In the present study, as in our previous studies (Stewardson et al. 2008, 2009, 2010a,b), age estimates are based on counts of growth layers in the dentine of canines.

The alternative dentition based technique of counting growth layers in the cementum of teeth (premolars) used by Arnould and Warneke (2002) on the Australian fur seal (*Arctocephalus pusillus doriferus*), the New Zealand fur seal (*Arctocephalus forsteri*) (McKenzie et al. 2007) and the Antarctic fur seal (*Arctocephalus gazella*) (Arnbom et al. 1992; Boyd and Roberts 1993) was not used in the present study. Oosthuizen (1997) compared the dentine and cementum techniques for aging South African fur seals of known age based on tagging and concluded that the dentine technique was more reliable and in particular concluded that the cementum techniques was not satisfactory for use on canines (cementum layer is too thin and fragile).

The counting Growth Layer Groups (GLG) in dentine has some significant limitations for aging fur seals. In the South African fur seal, it is not possible to determine chronological age of animals ≥12 y from growth layers in the dentine-GLG because of pulp cavity closure (Oosthuizen 1997; Stewardson 2001; Stewardson et al. 2008). The innermost dentine-GLG is the last layer laid down. There is a significant failure rate: in the present study about 1/3 of animals could not be aged after dentine sectioning because GLGs could not be resolved by microscopy.

The dentine and cementum based aging methods are destructive because teeth of specimens need to be extracted from skulls and sectioned. Sometimes neither the dentine-GLGs or cementum-GLCs can be properly distinguished after tooth sectioning. It might not be possible to get permission to do histological sectioning on the teeth of museum collections and some skulls might be in poor condition with missing, broken and decayed teeth. It appears that the dentine method is more suitable for dry museum skull specimens than the cementum method (Oosthuizen 1997; Stewardson et al. 1998). The cementum method is usually attempted on alcohol or formalin preserved teeth from recently dead or tranquilised animals (Arnbom et al. 1992; Boyd and Roberts 1993; Oosthuizen 1997; Arnould and Warneke 2002; Laws, Baird and Bryden 2002; McKenzie et al. 2007).

The estimated longevity of male South African fur seals in captivity is about 20 y (Wickens 1993) and wild male Australian fur seals live to at least 16 y (Arnould and Warneke 2002). Wild male New Zealand fur seals (*Arctocephalus forsteri*) in southern Australia are known to live to at least 19 y (McKenzie et al. 2007). Male Antarctic fur seals (*Arctocephalus gazella*) are also known to live to at least 16 y based on tag-aged animals (Arnbom et al. 1992; Boyd and Roberts 1993). Here we investigate the usefulness of suture closure criteria as an indicator of chronological age and physiological development in the male South African fur seal. Specific objectives were to: (i) describe the sequence of cranial suture closure and (ii) determine whether suture index corresponds to chronological age. There is no comparable information on development of sutures vs. age in the Australian fur seal, which is very closely related to the South African fur seal (Lento et al. 1997; Brunner 1998a,b; Brunner et al. 2002; Brunner 2004; Brunner et al. 2004; Stewardson et al. 2008, 2009, 2010a,b) and so any information gained on the South African fur seal would be useful for studies of the life history of the Australian fur seal (Arnould and Warneke 2002). Some caution is needed in applying information on South African fur seals to Australian fur seals. Adult male Australian fur seals are known to reach a marginally larger size than the South African variety and grow faster and perhaps live longer (Arnould and Warneke 2002; Stewardson et al. 2008, 2009).

MATERIALS AND METHODS

Abbreviations used in Text

Full Suture Closure (**FSC**), Partial Suture Closure (**PSC**), Suture Index (**SI**), Adjusted Coefficient of Determination (**R^2**).

Collection of specimens and morphometry

Male South African 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). Collection procedures are described in Stewardson et al. (2008, 2009). From this collection, 48 males had suture index (**SI**) information. Other skull data was available on 44 animals but suture information was missing on PEM2035, 2141, 2151 & 2252.

Thirty one (31) specimens were aged from incremental lines (called Growth Layer Groups, **GLG**) observed in the dentine of upper canines (Oosthuizen 1997; Arnould and Warneke 2002; Stewardson et al. 2008, 2009). Unfortunately, the GLG dentine-based aging method cannot age animals beyond 12 y old because of closure of the pulp cavity and so 10 of the 31 GLG-dentine-aged animals could only be classified as being ≥12 y old. Occasional individuals are found where 13 GLGs can be distinguished (PEM2151) and

Table 1: Suture Indices (SI*) for Male South African fur seals according to chronological age (y) based on tagging (Marine and Coastal Management (MCM collection), Cape Town) or dentition (Port Elizabeth Museum, PEM). Age classes are whole years (x) rounded to the nearest year. The suture scores were coded as ranging from 0-3 (fully open, 0; suture less than half closed, 1; suture more than half-closed, 2; fully closed, 3). Suture numbers (I to XI) are reconciled to those used by Brunner (1998a,b).

Suture & Suture N°	Age Classes (y)											
	Juvenile	Subadults						Adults				
	1	2	3	4	5	6	7	8	9	10	11	12
Basioccipito-basisphenoid (VI)	0,0	1,0	3,3	3,3,2,2,1,2,3	3,3	3,2,3,3,3,3	3,3,3,3,3,3,3,3,3	3,3,3,3,3,3	3,3,3	3	3	3
Occipito-parietal (I)	0,0	0,0	2,2	1,3,2,2,1,1,3	3,2	3,1,3,2,3,3	2,3,3,2,2,3,3,2,3	3,2,3,2,2,3	3,3,2	3	3	3
Coronal (V)	0,0	0,0	1,1	1,1,2,1,0,1,0	1,0	1,2,1,2,1,0	1,1,1,1,2,2,1,1,2	2,2,2,3,2,2	3,2,3	2	2	3
Interparietal (III)	0,0	0,0	0,0	1,1,1,1,0,1,0	1,1	0,2,1,1,0,1	1,1,1,1,1,2,0,1,2	2,1,2,1,0,1	3,1,3	2	1	3
Squamosal-jugal (X)	0,0	0,0	0,0	0,0,0,0,0,0,0	0,0	0,0,0,0,1,0	0,0,1,0,0,0,0,0,0	1,0,0,0,1,0	0,0,1	1	1	3
Premaxillary-maxillary (IX)	0,0	0,0	0,0	0,0,0,0,0,0,0	0,0	0,0,0,0,0,0	0,0,0,0,0,0,0,0,0	0,0,0,0,0,0	0,0,0	0	0	1
Maxillary (VII)	0,0	0,0	0,0	0,0,0,0,0,0,0	0,0	0,0,0,0,0,0	0,0,0,0,0,0,0,0,0	0,0,0,0,0,0	0,0,0	0	0	0
Squamosal-parietal (II)	0,0	0,0	0,0	0,0,0,0,0,0,0	0,0	0,0,0,0,0,0	0,0,0,0,0,0,0,0,0	0,0,0,0,0,0	0,0,0	0	0	0
Interfrontal (IV)	0,0	0,0	0,0	0,0,0,0,0,0,0	0,0	0,0,0,0,0,0	0,0,0,0,0,0,0,0,0	0,0,0,0,0,0	0,0,0	0	0	0
Basisphenoid-presphenoid (VIII)	0,0	0,0	0,0	0,0,0,0,0,0,0	0,0	0,0,0,0,0,0	0,0,0,0,0,0,0,0,0	0,0,0,0,0,0	0,0,0	0	0	0
Internasal (XI)	0,0	0,0	0,0	0,0,0,0,0,0,0	0,0	0,0,0,0,0,0	0,0,0,0,0,0,0,0,0	0,0,0,0,0,0	0,0,0	0	0	0
Suture Index (SI*)	**0,0**	**1,0**	**6,6**	**6,8,7,6,2,5,6**	**8,6**	**7,7,8,8,8,7**	**7,8,9,7,8,10,7,7,10**	**11,8,10,9,8,9**	**12,9,12**	**11**	**10**	**16**
Total N° Skulls = 42	**2**	**2**	**2**	**7**	**2**	**6**	**9**	**6**	**3**	**1**	**1**	**1**

so their minimum age is ≥13 y but such animals are rare. Attempts to age the remaining seventeen (17) animals from tooth sectioning were not successful.

The sample was supplemented with external body and skull measurements from 21 known-age animals (animals tagged as pups) from Marine and Coastal Management (MCM), Cape Town. Most specimens in the MCM collection had very complete data sets with the exception of MCM1809, which had only information on tag-age, suture indices for the skull sutures and condylobasal length (**CBL**). The data set for regression analyses of Age vs. Suture Index was therefore restricted to 42 skulls (21 age-tagged animals plus 21 GLG-dentine-aged animals < 12 y).

Sequence of suture closure

Eleven cranial sutures (Table 1) from 42 skulls with a definitive age, 10 skulls known to be from

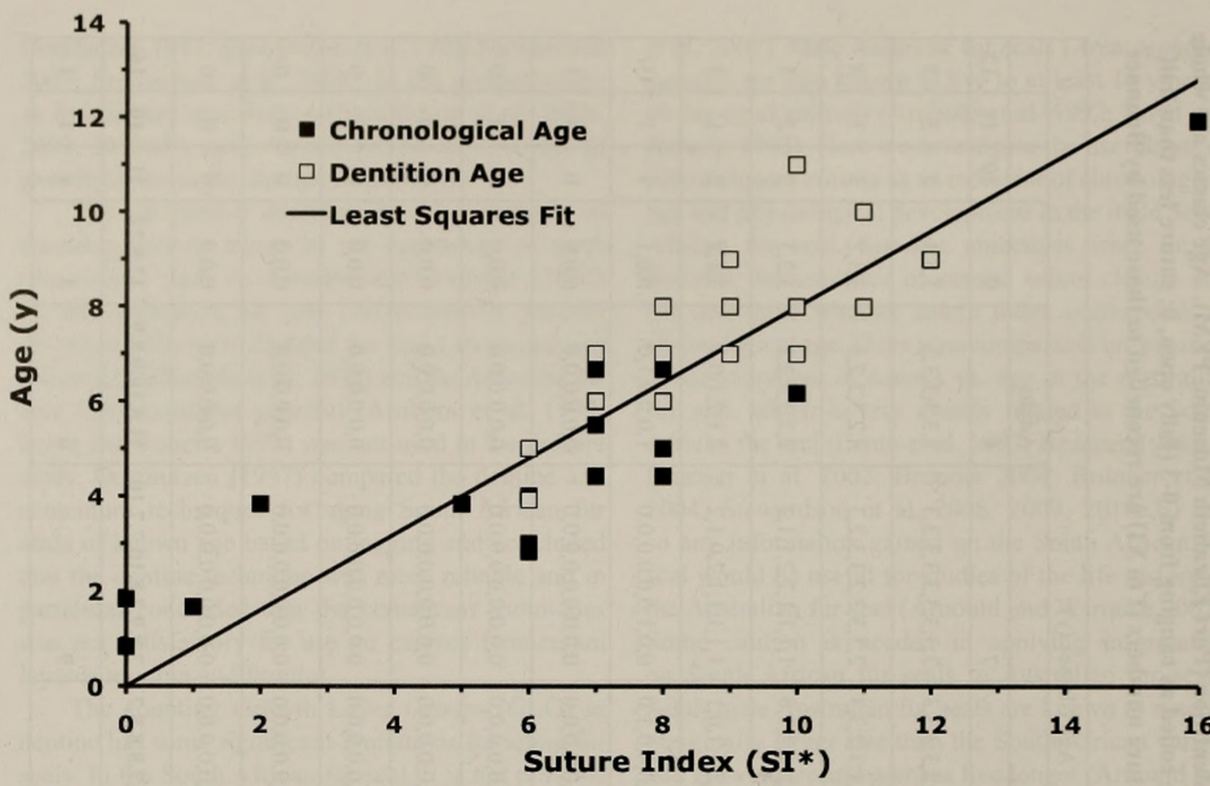

Figure 1. Regression analysis for age (y) of male South African fur seals vs. Suture Index (SI*) of male South African fur seals. Twenty one (21) seals (closed squares) were aged based upon being tagged as pups (with birthdate taken as 1 November). Twenty one (21) seals were aged based upon GLG-dentine (open squares). The fitted line is an ordinary least squares linear regression forced through the origin (0,0) (m = 0.7990 ± 0.02354, n = 42, r = 0.8887, p << 0.001).

males ≥12 y and 17 skulls of unknown age, were examined (n = 69). Sutures are conventionally assigned a value of 1-4, according to the degree of closure (1 = suture fully open; 2 = suture less than half-closed; 3 = suture more than half-closed; and 4 = suture completely closed) (Stewardson 2001; Brunner 1998a,b). Brunner (1998a,b) in her study of skull sutures in South African and Australian fur seals and the New Zealand Fur seal (*Arctocephalus forsteri*) measured nine sutures (did not record development of the Squamosal-jugal or Internasal sutures) and used a different numeration convention for numbering the sutures to those used by Stewardson (2001). For consistency with Brunner's work (Brunner 1998a,b, 2004; Brunner et al. 2002, 2004) her numeration conventions for sutures were adopted in the present study with the Coronal designated as suture (V), Interparietal as suture (III), Maxillary as suture (VII), Squamosal-jugal designated as suture (II) and the Internasal as suture (XI). Sutures were arranged in Table 1 in the approximate order of Partial Suture Closure (**PSC**) and Full Suture Closure (**FSC**).

To make curve fitting easier to interpret in the present study, the suture scores were recoded as ranging from 0-3 (fully open, 0; suture less than half closed, 1; suture more than half-closed, 2; fully closed, 3). These values were added to give a total suture index (**SI***), ranging from 0 (all sutures open) to 33 (all sutures closed). The special form of the suture index used in the present study is designated **SI***. The highest **SI*** on a male of definitive age was **SI*** = 16 for an individual 11 y 11 m old (MCM1809). The highest **SI*** readings were **SI*** = 22 for an animal ≥ 12 y based upon GLG-dentine (PEM1698) and another specimen (PEM1587) of unknown age.

Simple linear regressions were fitted using EXCEL routines and the SOLVER least squares fitting routine in EXCEL (Stewardson et al. 2008, 2009). General linear models and multiple linear regressions were fitted in Minitab15 (Minitab Inc., State College, PA 16801-3008, USA). Asymptotic errors of the fitted parameters were calculated by matrix inversion as previously described (Stewardson et al. 2008, 2009).

RESULTS

Suture Index vs. chronological age

The relationship between suture index (**SI***) and chronological age (Fig. 1, Table 1) was examined

Table 2: Analysis of Variance for a Multiple Linear Regression (MLR) of known age of Male South African Fur Seals on the following suture scores (0-3) for the Occipito-Parietal (OP), Coronal (C), Squamosal-Jugal (SJ) sutures (Equation 1). Based on 21 males with tag based ages and 21 with dentition based ages <12y. The Multiple Linear Regression was fitted as described by Cook and Weisberg (1999). The Students-t statistic and the calculated probability are for the null hypothesis that the value of each of the fitted parameters were zero. The relationship has a predictive range from 1.5542y (all sutures open, score 0) to 12.41y (all sutures closed, score 3).

Anova Table for Multiple Linear Regression

Source	df	SS	MS	F	P
Regression	3	219.541	73.180	52.73	< 0.0005
Residual Error	38	52.735	1.388		
Total	41	272.276			

Statistics on the fitted relationship: $y = 1.5542 + 1.0616xOP + 1.4538xC + 1.1033xSJ$

Predictor	Coefficients ± SE	Students t	P
Constant	1.5542 ± 0.4680	3.32	0.002
Occipito-Parietal (OP)	1.0616 ± 0.2156	4.92	< 0.0005
Coronal (C)	1.4538 ± 0.2386	6.09	< 0.0005
Squamosal-Jugal (SJ)	1.1033 ± 0.3490	3.16	0.003

using definitively known-age animals, 10 months to 11 y 11 m (n = 42) males. Twenty one (21) seals were aged based upon being tagged as pups (with birthdate taken as 1 November). Twenty one (21) seals were aged (1 to 11 y) based upon GLG-dentine as described previously (Oosthuizen 1997; Stewardson et al. 1998, 2008).

Regression analysis for age (y) of male South African fur seals vs. Suture Index (**SI***) is shown in Fig. 1. The fitted line is an ordinary least squares linear regression forced through the origin (0,0) or $y = mx$. This was justified because the y-intercept of a regression of the form $y = mx + b$ was not significantly different to zero. The slope $m = 0.7990 \pm 0.02354$, $n = 42$, $r = 0.8887$, $p << 0.001$. The standardized residuals vs. fitted values and the normal probability plot of the standardized residuals showed that the model assumptions held (errors independently and identically distributed according to a Normal distribution with zero mean and constant variance). The normality assumption was justified based upon the appearance of the normal probability plot.

Another way to approach estimating age is to fit a General Linear Model (GLM) to suture scores (Dobson 2001). A general linear model fit was made of age on the suture scores for the Basioccipito-basisphenoid (VI), Occipito-parietal (I), Coronal (V), Interparietal (III) and Squamosal-jugal (X) (five variables) as described by Cook and Weisberg (1999). The suture scores were treated as categorical data (strictly speaking they are ordinal which is ordered categorical). The reason the other suture variables were not included was because they were fully open for all definitively aged animals so provided no useful information for predicting age. The residuals vs. fitted values plot looked like a random scatter about zero so the model was adequate. The normal probability plot of the standardized residuals was approximately linear so the normality assumption held. Plotting the coefficients for each level of the suture considered against level the relationship was roughly linear for each suture so we could treat the sutures as continuous variables even though technically they are ordinal variables. This allowed us to fit a multiple linear regression model to the data with age as the dependent variable and the five suture variables as the independent variables. Not all five sutures were needed in the model. A multiple F-Test showed that we could collapse the model with all five predictors in it to a simpler model (p-value = 0.61) with only 3 suture scores plus a constant. The final multiple linear regression model fitted to the data was;

Predicted Age (y) =

$$1.5542 + 1.0616xOP + 1.4538xC + 1.1033xSJ$$

Equation 1

where, OP is the suture score for the Occipito-parietal (I), C is the score for the Coronal (III) and SJ is the score for the Squamosal-jugal (X). The Coefficient of Determination (R^2) was 0.8060 and the Adjusted Coefficient of Determination was 0.7910 (adjusted for fitting 3 parameters, see Cook and Weisberg 1999).

The ANOVA on the multiple linear regression and the asymptotic errors of the fitted parameters calculated by matrix inversion are shown in Table 2. Inference was possible because the residuals vs. fitted values plot looked like a random scatter about zero

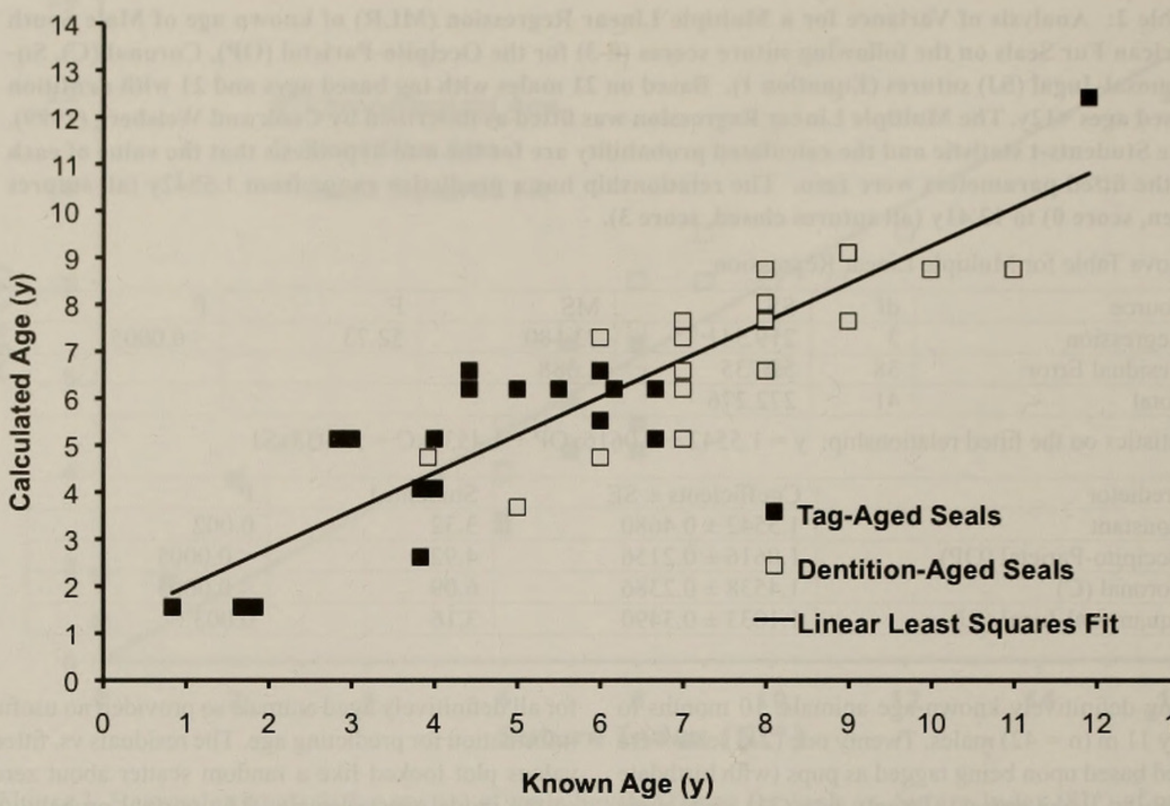

Figure 2. Calculated age using multiple linear regression of suture scores vs. known age (n = 42) of male South African fur seals. Suture scores were graded from 0 to 3 and the predicted age calculated using Equation 1 using data on closure for the Occipito-parietal (I), Coronal (V) and Squamosal-jugal (X) sutures. The minimal possible predicted age was when all sutures had a suture score of zero and maximum when all sutures had a score of 3. The predicted age was within ±1 y in 26 of 42 animals, within ±1.5 y in 34 of 42 animals and all predicted ages were within ±2 y.

and the normal probability plot of the standardized residuals was approximately linear so the normality assumption held. All predictions of age lie between 1.5542 (all sutures with a score of zero) and 12.4103 (all three sutures with a score of 3) so we could use this fitted model to predict the age of subadults and adults. The maximum possible predicted age using Equation 1 is 12.41; inclusion of the 5 suture variables initially used for this analysis only extends the predicted age to 12.65 y.

Fig. 2 shows a plot of predicted age using the multiple linear regression above (Equation 1) vs. known age. The multiple linear regression is able to predict ages within about ± 1 y for individuals 1 to 12 y. There is a good linear relationship between predicted age (y) and known age (y), ($r = 0.8980$, $p << 0.001$). The accuracy of the predicted age varies from 1.9 ± 0.4 y for 1 year-olds to 10.9 ± 0.86 y for 12 y-olds. Predicted age was within ±1 y for 62% of all animals of known age, within ±1.5 y for 81% and within ±2 y for all animals of known age.

Sequence of Suture Closure

The sequence of partial suture closure (**PSC**) differed from the sequence of full suture closure (**FSC**) with fusion beginning at different ages and some sutures taking longer to close than others (Tables 1 and 3).

For the range of available specimens using classification analysis, the sequence of beginnings of **PSC** according to chronological age was Basioccipito-basisphenoid (VI) (**PSC** at 2 y), Coronal (V) (**PSC** at 3 y), Occipito-parietal (I) (**PSC** at 3 y), Interparietal (III) (**PSC** at 4 y), Squamosal-jugal (X) (**PSC** at 6 y) and Premaxillary-maxillary (IX) (**PSC** at 12 y). Considering that the Basioccipito-basisphenoid suture (VII) was fully closed in nearly all animals at 3-4 y, **PSC** would occur at 1 or 2 y, before or at the same time as the Coronal (V). The Squamosal-parietal (II), Interfrontal (IV), Basisphenoid-presphenoid (VIII) (sutures of the brain case), Internasal (XI) and Maxillary (VII) (sutures of the face), showed no signs of partial closure in animals less than 11 y 11 m. Even

Table 3: Standard body length (SBL), Condylobasal length (CBL), SI* and Age Estimations for Male South African fur seals using the Age (y) vs. SI* linear regression relationship (Fig. 1) and the multiple linear regression approach (Equation 1, Fig. 2) which gives an age maximum of 12.4 y. The 17 males with ages marked (*) had no tag or dentition-based age; specimens marked ${}^{3}12$ or ${}^{3}13$ (n = 10) were known to be 12 y or older based upon dentition. Predicted ages based upon SI* values >16 are only provisional because they are extrapolations and are marked (?).

Museum N°	SBL (cm)	CBL (mm)	Suture N° (as for Table 1; those used for multiple linear regression marked in **bold**)											Suture Index (SI*)	Age (y)	Predicted Age (y ± SE)	Age (y) Multiple Linear Regression
			VI	**I**	V	III	**X**	IX	VII	II	IV	VIII	XI				
PEM898	200	*	3	**3**	**2**	2	**2**	1	1	0	0	1	1	16	*	12.78 ± 0.38	9.85
PEM916	91	159.5	1	**0**	**1**	0	**0**	0	0	0	0	0	0	2	*	1.60 ± 0.05	3.01
PEM917	104	176.6	1	**0**	**1**	0	**0**	0	0	0	0	0	0	2	*	1.60 ± 0.05	3.01
PEM951	170	226.5	3	**2**	**1**	0	**0**	0	0	0	0	0	0	6	*	4.79 ± 0.14	5.13
PEM958	190	240.9	3	**3**	**1**	1	**1**	0	0	0	0	0	0	9	*	7.19 ± 0.21	7.30
PEM975	172	232.2	3	**3**	**2**	0	**0**	0	0	0	0	0	0	8	*	6.39 ± 0.19	7.65
PEM1453	193	*	3	**3**	**1**	0	**0**	0	0	0	0	0	0	7	*	5.59 ± 0.16	6.19
PEM1560	201	241.3	3	**3**	**1**	3	**0**	0	0	0	0	0	0	10	*	7.99 ± 0.24	6.19
PEM1587	192	265.3	3	**3**	**3**	3	**3**	2	2	2	1	0	0	22	*	17.58?	≥ 12.4
PEM1892	185	242.9	3	**3**	**2**	1	**0**	0	0	0	0	0	0	9	*	7.19 ± 0.21	7.65
PEM2035	*	*	1	**0**	**1**	0	**0**	0	0	0	0	0	0	2	*	1.60 ± 0.05	3.01
PEM2137	118	194.9	1	**1**	**1**	0	**1**	0	0	0	0	0	0	4	*	3.20 ± 0.09	5.17
PEM2198	104.8	186.4	3	**0**	**1**	0	**0**	0	0	0	0	0	0	4	*	3.20 ± 0.09	3.01
PEM2201	103	171.1	2	**0**	**0**	0	**0**	0	0	0	0	0	0	2	*	1.60 ± 0.05	1.55
PEM2238	96	176.5	2	**1**	**0**	0	**0**	0	0	0	0	0	0	3	*	2.40 ± 0.07	2.62
PEM2253	152	230.8	3	**3**	**2**	2	**0**	0	0	0	0	0	0	10	*	7.99 ± 0.24	7.65
PEM2254	146	226.5	3	**3**	**1**	0	**1**	0	0	0	0	0	0	8	*	6.39 ± 0.19	7.30
PEM1507	198	260.7	3	**3**	**2**	3	**2**	2	2	2	1	0	0	20	≥12	15.98?	9.85
PEM1698	190	*	3	**3**	**3**	3	**3**	2	2	2	1	0	0	22	≥12	17.58?	≥ 12.4
PEM1879	200	259.2	3	**3**	**3**	2	**2**	2	1	1	1	0	0	18	≥12	14.38?	11.3
PEM1882	180	248.3	3	**3**	**3**	3	**2**	2	0	0	0	0	0	16	≥12	12.78 ± 0.38	11.3
PEM1890	192	258.5	3	**3**	**3**	2	**2**	1	1	1	1	0	0	17	≥12	13.58?	11.3
PEM1895	188	263.9	3	**3**	**3**	2	**3**	1	2	2	0	0	0	19	≥12	15.18?	≥ 12.4
PEM2049	174	262.7	3	**3**	**3**	3	**1**	1	1	0	1	0	0	16	≥12	12.78 ± 0.38	≥ 12.4
PEM2132	194.8	257.8	3	**3**	**3**	3	**2**	2	2	1	1	0	0	16	≥12	12.78 ± 0.38	10.2
PEM2141	*	250.3	3	**3**	**3**	3	**1**	1	1	1	1	0	0	20	≥12	15.98?	11.31
PEM2151	*	262.7	3	**3**	**3**	3	**3**	0	1	0	0	0	0	17	≥13	13.58?	10.2

in the very old males (≥ 12 y) there were no signs of closure in the Basisphenoid-presphenoid (VIII) or Internasal (XI) (Table 3).

The sequence of **FSC** according to known chronological age was Basioccipito-basisphenoid (VI), Occipito-parietal (I), Coronal (V), Interparietal (III) and finally Squamosal-jugal (X) (Table 1). With the exception of the Squamosal-jugal (X) these are sutures of the brain case. The Basioccipito-basisphenoid (VI) was fully closed at 3-4 y in nearly all animals. The Occipito-parietal (I) was fully closed in some animals as early as 4 y-old class. The Coronal (V) was fully closed in one 8 y-old, two 9 y-olds and one 12 y-old. The Interparietal (III) was fully closed in two 9 y-old animals and one 12 y-old. The Squamosal-jugal (X) was fully closed in the one animal in the 12 y-old class where its age was based upon tagging. All other definitively aged animals had no closure or only partial closure of the Squamosal-jugal (X). The Maxillary (VII), Squamosal-parietal (II), Interfrontal (IV), Basisphenoid-presphenoid (VIII) and Internasal (XI) showed no signs of even partial closure in definitively aged animals (Table 1) but some partial closure of these sutures were observed in very old animals with ages greater than or equal to 12 y (Table 3).

Although the sutures and their pattern of closure were clearly related to each other and to chronological age, the sequence of closure was not sufficiently close to be used as a reliable technique for estimating chronological age (Table 1). Unfortunately, the data set was too small to further develop such a classification system in the present study.

DISCUSSION

Limitations of Dentition-Based Ageing of Skulls

There are two commonly used methods of aging seals using dentition: counting growth layers in the dentine or counting growth layers in the cementum. The geometry of deposition of dentine and cementum is different: dentine is deposited from the outside to the inside of the tooth and hence is limited by closure of the tooth pulp. Once the pulp is closed no further layers of dentine can be deposited and so dentine layering has determinant growth (McCann 1993). Cementum is deposited by the periodontal membrane surrounding the root of the tooth and so the innermost layer is the oldest and the outermost layer is the newest. Its growth is indeterminate.

In the South African fur seal, it is not possible to determine chronological age of animals ≥12 y from growth layers in the dentine (called Growth Layer groups or GLG) because of pulp cavity closure (Oosthuizen 1997; Stewardson 2001; Stewardson et al. 2008) and so cannot be used to estimate ages of animals over the full life-span of these seals (Wickens 1993). Male Australian fur seals up to 16 y old were identified by Arnould and Warneke (2002) using the cementum-ageing method. It is important that Arnould and Warneke (2002) were able to identify very old females up to 26 y old and so it is likely that the technique would be useable for males over their entire lifespan. Arnbom et al. (1992) were able to correctly age Antarctic fur seals (*Arctocephalus gazella*) using the cementum technique on animals with known ages of 16 y and McKenzie et al. (2007) could age male New Zealand fur seals (*Arctocephalus forsteri*) up to 19y.

Lack of awareness of the limitations of dentine-based aging can lead to mistakes in aging animals and hence erroneous life tables. Dickie and Dawson (2003) did not take pulp closure into account in their dentine-based aging of New Zealand fur seals and concluded that the oldest individuals in their study were 12 y old. In an independent study McKenzie et al. (2007) using the cementum method were able to identify males that were 19 y old and so it is probable that some individuals in the study by Dickie and Dawson (2006) aged using the dentine-GLG method were actually older than 12 y. The crucial limitations of the dentine aging method are well illustrated by the example of the crabeater seal (*Lobodon carcinophagus*). In the crabeater seal the dentine method is only useable for animals up to about 10 y old because of pulp cavity closure but the cementum technique can be successfully used to age animals up to 39 y (Laws et al. 2002). The cementum technique needs reassessment in South African fur seals.

Suture closure

Examination of suture index (**SI***) relative to **SBL** supported the sequence of **FSC** derived from chronological age: (i) full closure of the Coronal (V) occurs at about the same time or slightly before that of the Interparietal (III), and (ii) full closure of the Maxillary (VII) occurs after full closure of the Squamosal-jugal (X). The order of closure appears to be, Basioccipito-basisphenoid (VI), Occipito-parietal (I), Coronal (V), Interparietal (III), and then the Squamosal-jugal (X) (suture sequence: 6,1,5,3,10). The Premaxillary-Maxillary (IX) showed no signs of closure in any of the definitively aged animals except for the oldest specimen, which was 11 y 11 m old. In our sample of skulls there were no signs of closure in definitely aged animals (≤12 y) of the Maxillary (VII), Squamosal-parietal (II), Interfrontal (IV), Basisphenoid-presphenoid (VIII) or Internasal (XI) although some animals aged as ≥12 y based upon GLG-dentine did have partial closure of these sutures (Table 3).

With the exception of the Squamosal-parietal (II), our study shows that the sutures of the brain case [Basioccipito-basisphenoid (VI), Occipito-parietal (I), Coronal (V) and Interparietal (III)] close before those of the face [Squamosal-jugal (X) and Premaxillary-maxillary (IX)]. Brunner (1998a) found a similar, but not identical, general pattern in the Australian fur seal (suture sequence: 6,1,3,5,2,7,9,8,4) and the New Zealand fur seal. As with other mammals, the brain case attains full size early in development (neural growth pattern) because early maturation of the brain case is essential for nervous control of the body (Moore 1981).

The sequence of **FSC** reported by Rand (1949) based on male South African fur seals of unknown chronological age was: Basioccipito-basisphenoid (VI), Occipito-parietal (I), Interparietal (III), Coronal (V), Squamosal-parietal (II), Premaxillary-maxillary (IX); Interfrontal (IV) and Basisphenoid-presphenoid (VIII) in fully mature males (**SBL** ≈ 217 cm); and finally the Internasal (XI) in very old emaciated males (SBL ≈ 223 cm). The Maxillary suture (VII) was not examined and so Rand's **FSC** suture sequence was: 6,1,3,5,2,9,4,8,11. This **FSC** sequence is similar to that found by Brunner (1998a) for the Australian fur seal (suture sequence: 6,1,3,5,2,7,9,8,4) but differs from that found in the present study in the order of closure of the Interparietal (II) and Coronal (V). The sequence of **FSC** for the first 4 sutures was supported by the present study, and confirmed that certain sutures do not fully fuse until the animal is ≥12 y (Premaxillary-maxilla (VI), Maxillary (VII), Interfrontal (IV), Basisphenoid-presphenoid (VIII) and Internasal (XI). It is interesting to note that the **PSC** and **FSC** closure sequences found in the present study are similar to but not identical to those found for the Australian fur seal (**PSC**: suture sequence: 1,5,6,2,3,7,9,4,8; **FSC**: suture sequence: 6,1,3,4,2,7,9,8,4) and considerably different to sequences found in the New Zealand fur seal (Brunner 1998a,b) and other fur seals (Brunner 2004; Brunner et al. 2004). Our suture closure sequences are more reliable than most other reported suture closure sequences of fur seals because they are largely based on known-age males.

One major difference between closure patterns of sutures in South African fur seals compared to suture closure patterns in Australian fur seals may be in the maximum degree of closure found in the animals. On the Brunner scale (Brunner 1998a,b) the maximum suture index score was 4 × 9 = 36 when all 9 sutures were closed. Brunner (1998a) recorded several animals with suture scores greater than 34. In the present study on South African fur seals, no animal closely approached **FSC** of all the sutures examined. On Brunner's scale and taking into account only the 9 sutures used in her study, the two animals with the highest suture indices in the present study were PEM1698 (≥12 y) with a Brunner-scale suture index of 26 and PEM1587 (unknown age) with a Brunner-scale suture index of 28. These suture indices are well short of the 36 maximum score for 9 sutures on a 1-4 scoring scale. The data of Arnould and Warneke (2002) shows that male Australian fur seals may be considerably longer-lived than their South African counterparts and their data also supports Brunner (1998a) who contended that Australian fur seals have a slightly different growth pattern to South African fur seals.

Orr et al. (1970) found that in male *Zalophus californianus,* California sea lion, the sequence of **PSC** and **FSC** (n = 9 sutures) differed slightly from that found in the South African fur seal. The sequence of **PSC** was: Basioccipito-basisphenoid (VI), Coronal (V), Squamosal-parietal (II), Occipito-parietal (I), Interfrontal (IV), Interparietal (III), Premaxillary-maxilla (IX), Basisphenoid-presphenoid (VIII) and finally the Maxillary (VII), while the sequence of **FSC** was: Basioccipito-basisphenoid (VI), Occipito-parietal (I), Interparietal (III), Squamosal-parietal (II), Coronal (V), Basisphenoid-presphenoid (VIII) and finally the Interfrontal (IV)/Premaxillary-maxillary (IX)/Maxillary (VII), with all sutures fully closed by 15 y (n = 35 males, 1-15 y). Thus, the suture index (**SI***) of the California sea lion does reach an asymptote, whereas this does not seem to occur in the South African fur seal although it does seem to occur in both the Australian fur seal and the New Zealand fur seal (Brunner 1998a,b). No wild South African fur seal male appears to be recorded where all the skull sutures have been found to be fully closed (present study and Rand 1949). Perhaps so few animals reach ages much beyond 12 y that it would be unlikely to find a tagged animal of such an age. Boyd and Roberts (1993) in their study of the life history of the Antarctic fur seal on South Georgia found that the average age at death of a sample of 724 male seals was only 7.69 ± 1.9 (SD) y and were able to find only two 14 y-olds and one 16 y-old.

In male *Callorhinus ursinus,* Northern fur seal, the age at which the sutures begin to close and the length of time taken for sutures to fully close was slightly different than in the South African fur seal (Scheffer and Wilke 1953; present study). For example, the Basioccipito-basisphenoid (VI) closed between 2 and

6 y; the Occipito-parietal (I) closed between 2 and 6 y; and the Interparietal (III) closed between 4 and 7 y (n = 121 males, 1-7 y). Other sutures were not examined.

Differences in growth rates/patterns and considerable individual variation between animals of similar age, and small sample sizes, would account for observed discrepancies within and between species noted by Brunner (1998a,b), Brunner (2004) and Brunner et al. (2002, 2004).

Suture Index as an indicator of chronological age

We have concluded that in male South African fur seals, suture index (**SI***) cannot be regarded as a highly reliable technique for estimating chronological age. The suture index (**SI***) has been shown to be a useable estimator of the age of male South African fur seals but is not as accurate as GLG-dentine (Oosthuizen 1997; Stewardson et al. 1998, 2008). This is in agreement with comprehensive studies on humans where date of birth and date of death are usually well documented (McKern and Stewart 1957; McKern 1970). No suture index (**SI***) vs. age information appears to be available on Australian or New Zealand fur seals.

The limitations of the plot of **SI*** vs. Age (Fig. 1) are that there is a significant spread of data points around the regression line and the oldest animal in the data set was only 11 y 11 months old. The relationship between **SI*** and Age is not known for animals older than 12 y or only about 1/2 to 2/3 of the estimated lifespan of South African fur seals (Wickens 1993). Nevertheless, Table 3 shows that Age vs. **SI*** does not appear to suddenly reach an asymptote at **SI*** values only slightly beyond the maximum **SI*** value for an animal of definitively known age (Fig. 1, Tables 1 and 2). The linearity of the **SI*** vs. Age regression does not appear to level off in old animals but it would be inappropriate to confidently extrapolate the curve for deducing the age of animals with a **SI*** value much greater than 16. Some very old animals had suture indices as high as 22 (PEM1587 & PEM1698), which by extrapolation implies an age of about 17.5 ± 0.5 y, but such age determinations should be taken as *only provisional*. Orr et al. (1970) found that suture index vs. age was asymptotically curvilinear in old male California sea lions. In most mammals (Morris 1972) and in humans (McKern and Stewart 1957; McKern 1970; Sinclair 1973) it is known that suture closure does not continue at a linear rate in old age. Perhaps a curvilinear model might prove to be more appropriate if **SI*** data on very old animals becomes available.

Table 3 shows a summary of our attempts to use the simple linear regression of age vs. **SI*** to predict the ages of some specimens where no age information was available or where the dentine-GLG technique could only estimate their age as greater than or equal to 12 y. The Age vs. **SI*** regression (Fig.1) is useful for predicting the age of animals of unknown age (n = 17) and some animals with a GLG-dentine-based age of ≥12 y (n = 10). Six (6) of the ten animals known to be at least 12 y (based upon GLG-dentine) had **SI*** values of 16 or 18 and so their ages can be estimated to be about 13 to 15 y old with a reasonable degree of confidence (Table 3). The remaining four (4) males had **SI*** values ranging from 19 to 22, indicating that they must be very old animals. Sixteen of the 17 animals with unknown age have **SI*** values within the range of the regression fit (**SI*** = 0 to 16) and so valid estimates of their ages could be made (Table 3).

Multiple linear regression (Equation 1) appears to give useful estimates of the ages of animals based on closure of three sutures (Fig. 2; Tables 2 and 3). The predictive range of Equation 1 is 1.55 y (all 3 sutures open) to 12.41 y (all 3 sutures closed). There are no pups and only two yearlings (aged 6 to < 18 months) in the data set. All fur seals with ages defined only as being greater than 12 y (based upon GLG-dentine, n = 17) and hence not used to generate Equation 1, were correctly predicted to be adults at least 9.85 y (Table 3). If we had seals older than 12 y that were accurately aged, it should be possible to extend the model using closure of additional sutures to estimate ages greater than the limits imposed by using only 3 sutures. Including later-closing sutures in an extended model it may be possible to reliably predict ages of older males using suture index (**SI***) or a multiple linear method. This would help in life-history and population studies of fur seals.

Suture Information and Age Class

Data on closure of some sutures are useful for classifying animals into pup/juvenile, subadult and adult classes and so is an indicator of age class in male South African fur seals (Table 1). The Basioccipito-basisphenoid suture (VI) located at the base of the skull is open (Suture score = 0) in pups and juveniles and is completely closed (score = 3) or more than 50% closed in all males older than 3 y. The sequence of closure of the Basioccipito-basisphenoid suture (VI) in South African fur seals exhibited little variability, with complete or nearly complete fusion evident at 3 or 4 y. Examination of this suture reveals the following: (i) suture open = male ≥ 3 y old; (ii) suture fully closed = male 3-4 y or older and male has reached puberty (Stewardson et al. 1998). Complete closures of the Basioccipito-basisphenoid (VI) + Occipito-parietal (I) + Coronal (V) + Interparietal (III) sutures only occurs in adult males > 7 y.

CONCLUSIONS

In male South African fur seals the sequence of partial suture closure (**PSC**) is different to the sequence of full suture closure (**FSC**). Sutures of the skull begin to close at different ages and the length of time taken for each suture to fully close is different. The sequence of **FSC** is Basioccipito-basisphenoid (VI), Occipito-parietal (I), Interparietal (III)/Coronal (V) and finally the Squamosal-jugal (X) in males ≥ 12 y. Suture index (**SI***) is not a very accurate indicator of chronological age (error ≈ ± 1-1.5 y), sutures close faster in some individuals than in others and sutures do not close in a definitive order, they close in different orders in different individuals. Thus suture closure statistics shown in Table 1 demonstrate that using suture closure sequences to determine relative ages of fur seals has the underlying flaw that sutures do not close in a definitive order (cf. Rand 1949, 1956; Brunner 1998a,b; Brunner et al. 2004). Based upon the data set currently available, **SI*** can be used to estimate ages of males up to about 14 y. If the average life span of South African fur seals is similar to that of the Antarctic fur seal (Boyd and Roberts 1993; Boyd et al. 1995) then a 0 - 14 y useful age range would be sufficient to be able to age the vast majority of skulls of dead animals. The Basioccipito-basisphenoid (VI) can be used as an indicator of age class for pups/juveniles and subadults and combined with closure scores of other sutures adults can be distinguished from subadults. In principle, multiple linear regression of age vs. suture scores of several individual sutures can be used to estimate age. Multiple linear regression is likely to give more accurate estimates of age than the cruder suture index (**SI***) but inherently requires a large data set because several independent variables have to be fitted to the data set. Since we know that some sutures only close in very old males (Table 3), the use of suture information does offer a means of estimating the age of very old males but suture data on old males of known age is needed to extend the method to the full lifetime of the seals. However, in order to age very old animals using a multiple linear regression approach more suture variables would have to be added to the 3 suture scores used in Equation 1 and Fig. 2 because in very old animals all of these sutures have completely closed (Table 3). A multiple linear regression equation to predict ages over the full lifespan of male fur seals would probably need 9 to 11 suture scores as variables. Future efforts should be made to develop the cementum-dentition method of determining age in South African fur seals.

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