African Journal of Marine Science 2007, 29(2): 161–176
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AFRICAN JOURNAL OF
MARINE SCIENCE
ISSN 1814–232X
doi: 10.2989/AJMS.2007.29.2.2.185

Making sense of censuses and dealing with missing data: trends in pup counts of Cape fur seal *Arctocephalus pusillus pusillus* for the period 1972–2004

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Trends in the population of Cape fur seals *Arctocephalus pusillus pusillus* were estimated from counts of pups on aerial photographs of colonies taken between 1972 and 2004 to determine trends in the overall population and subpopulations. Incomplete coverage resulted in missing data in some years. Various methods of determining proxy values for missing data were assessed, and it was concluded that different methods were applicable to Namibian and South African colonies. This reflected variation in trends of pup counts between the countries, which was associated with differences in productivity between the southern and northern Benguela ecosystems. In Namibia, temporal changes in pup numbers were non-linear in some years and there was correspondence in fluctuations at most colonies. This appeared to be on account of an effect of periodic, wide-scale prey shortages that reduced birth rates. There was a northward shift in the distribution of seals in the northern Benguela system. In South Africa, pup counts were much less variable between years, probably on account of a relative stability of food supply. A linear approach was therefore suitable for determining proxy values for missing data at South African colonies. Pup counts suggest that there has been little change in the overall population of the Cape fur seals since 1993, when it was estimated at about two million animals.

Keywords: Cape fur seal, census, missing data, Namibia, pup numbers, South Africa, trends

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Introduction

Cape fur seals *Arctocephalus pusillus pusillus* occur along the southern and western coasts of southern Africa (Figure 1). The size of the seal population before the arrival of Europeans in southern Africa is unknown, but it is thought that seals occurred on most, if not all, of the islands off South Africa and Namibia (Shaughnessy 1982, 1984). However, seal hunting (sealing) between the 17th and 19th centuries caused a marked decline in the population size (Rand 1952, Shaughnessy and Butterworth 1981). The effects of uncontrolled sealing, together with the activities of guano collectors and the management of many islands for guano and other seabird products after the discovery of guano, resulted in the extirpation of seals from many of their former breeding locations. In general, the remaining seals were restricted to islets not utilised by guano-producing birds, and not easily accessible to seal hunters (Rand 1952). By the beginning of the 20th century, Cape fur seals had disappeared from at least 23 offshore locations (Best and Shaughnessy 1979, Shaughnessy 1982). At its most reduced level, the population size is thought to have been below 100 000 individuals (Shaughnessy and Butterworth 1981).

The most recent assessment of the Cape fur seal population size, estimated about 2 million animals (including pups) at the beginning of 1993 (Butterworth *et al.* 1995), indicating that the population had grown about 20-fold during the 20th century. The recovery in numbers followed the imposition of legal controls on sealing at the beginning of the 20th century, and has been perceived as the normal response of a population recovering from overexploitation (Shaughnessy and Butterworth 1981). The recovery was notwithstanding that seals have been unable to re-colonise most of the offshore locations from where they were previously extirpated (Shaughnessy 1984). Instead, new breeding colonies that formed on the mainland during the 20th century have accounted for most of the growth (Rand 1972). It is thought that mainland-based seal breeding colonies were not viable before the arrival of Europeans in southern Africa, owing to the presence of terrestrial mammal predators, not only lions *Panthera leo*, brown hyaenas *Hyaena brunnea* and black-backed jackals *Canis mesomelas*, but also humans such as early hunter-gatherers (Shaughnessy and Butterworth 1981). The large mainland colonies have been established

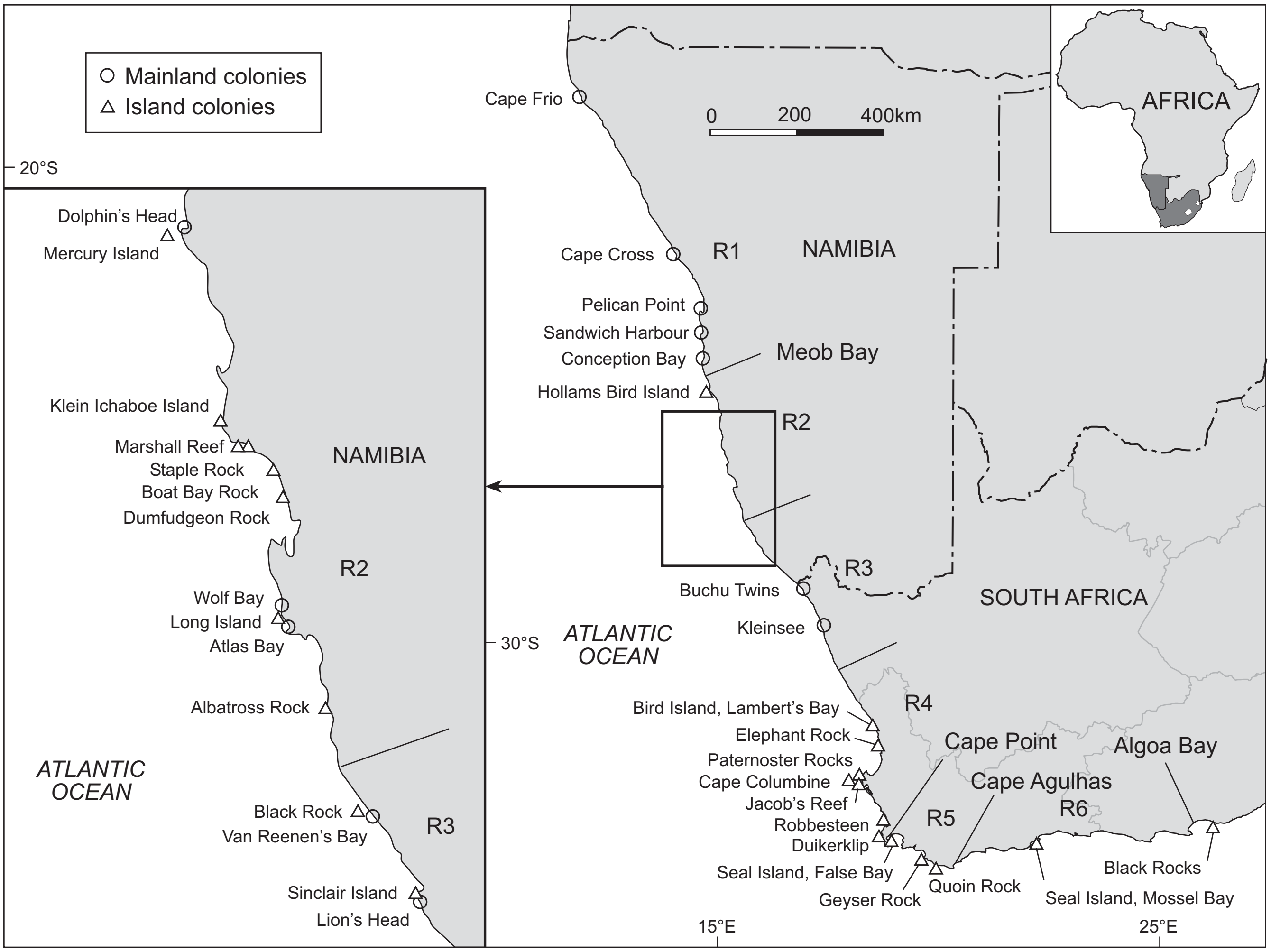

Figure 1: Distribution of Cape fur seal in South Africa and Namibia, showing mainland and island breeding colonies. Regions 1–6 are indicated as R1–R6, and separated by straight lines drawn inland from the coast

in the coastal diamond-mining zones of Namibia and South Africa, where terrestrial seal predators had been largely exterminated and human access and disturbance was minimised (Rand 1972).

With the seal population estimated to have doubled in size between 1970 and 1990, it was mooted that the seemingly unlimited breeding space presented by mainland locations, compared with offshore locations, may have caused the seal population size to surpass its pre-sealing level (Griffiths *et al.* 2005). The outcomes of modelling exercises conducted in 1990, around the time when a moratorium was placed on seal harvesting in South Africa, predicted that the seal population would again double within 10 years, and treble in 20 years, unless the population was subjected to density dependent effects (e.g. food deprivation) or further sealing (Butterworth and Wickens 1990, Butterworth *et al.* 1991). Since then, however, sealing has continued off Namibia, where approximately 60% of the Cape fur seal population occurs (Wickens *et al*. 1991), but not in South Africa. Furthermore, since 1993, there have been at least two mass die-offs of seals in Namibia, apparently related to the effects of unfavourable environmental conditions on the distribution and abundance of their prey (Roux 1998, Roux *et al.* 2002). The first, in which tens of thousands of seal pups and thousands of adults starved to death in 1994–1995 (Roux 1998), was the largest mass die-off recorded for any seal species (Harwood 2002).

Consequently, there is interest in recent trends of the seal population. On the one hand, there is concern for the conservation status of the population, in view of the mass die-offs and continued harvesting in Namibia. On the other hand, many fishers motivate for a reduction in seal numbers, because they perceive this as benefiting their livelihoods (Wickens *et al.* 1992, Best *et al.* 1997). Moreover, seabird conservationists claim that the seal population at the start of the 21st century exceeds its pristine level, and are concerned that seals negatively impact locally breeding seabird species classified as 'Threatened' according to IUCN criteria (e.g. Crawford and Robinson 1990, Ward and Williams 2004).

Censuses of Cape fur seals have been conducted frequently since the early 1970s. The censuses were based on counts of pups on aerial photographs, taken systematically of seal breeding colonies when the numbers of newborn pups of the year were expected to be at their maximum. Although these censuses inherently underestimate the numbers of pups in each colony, Shaughnessy (1987) found them to be useful indicators of pup production. However, where trends in pup numbers over time are determined from collective pup counts of colonies, complete aerial coverage in each census year is desirable. Where this was not achieved and counts of one or more colonies are lacking, values need to be inferred for the missing data. Otherwise, censuses of different years are not directly comparable, particularly if one or more of the larger breeding colonies are concerned. Missing data is a recurrent problem in the time-series of Cape fur seal censuses, and the problem has been approached differently between some previous assessments of the population (e.g. Butterworth *et al*. 1987, 1995). However, no attempt has been made to empirically assess the accuracy of alternative approaches for estimating missing data values. In this study, we assessed the accuracy shown by four different methods in approximating the correct values of available counts, with a view to determining the best-suited approach. Once this was achieved, and missing data values were inferred accordingly, the trends in pup numbers of the whole population and various subpopulations were investigated, based on all the censuses that have been completed to date (1971–2004). The pup count trends are interpreted and the relationship between recent trends (especially since 1993) and the status of the seal population (all age-classes inclusive) are discussed.

Material and Methods

Background

The procedure for censusing the Cape fur seal pup population using aerial photography is detailed by Shaughnessy (1987). Briefly, near vertical, serial overlapping photographs are taken from aircraft flying parallel flight paths over colonies at a height of c. 100m. For large colonies, high altitude pictures (c. 300m) of the colony are also taken, to assist with fitting of the lower altitude prints to map the colony. The timing of photographing is standardised, taking place during 16–22 December each census year, except where otherwise indicated (see Appendix).

After printing, pictures are laid out in frame sequence and a photographic mosaic of each colony is arranged. Boundaries between neighbouring, overlapping photographs are delineated on each photograph, using landmarks or seals that are in common between the photographs, to prevent counting repetition. Duplicate photographs are eliminated. The seal pups on each photograph are counted by two people, and the arithmetic mean of the counts is taken.[1] In the few instances where counts differ by more than 20%, additional counts are conducted until two counts are within 20% of each other, and the other counts are discarded. Whereas this approach precludes estimates of variance, it means that the amount of variability between the counts used is always <20%. Once all photographs of a colony are counted, the means are added together to get the colony's total count.

In this study, we referred to censuses by the year in which the pup cohort under observation was weaned, not the year in which the census occurred. For example, the census of December 2003 refers to the 2004 census. Between 1971 and 2004, a census was conducted in all but five years, with the number of colonies that were covered varying between census years (see Appendix). Seal colonies were also photographed in 2005, 2006 and 2007, but the pup counts are as of yet incomplete and therefore unavailable for this study.

Breeding and non-breeding colonies

Oosthuizen and David (1988) distinguished between breeding and non-breeding seal colonies. They classified non-breeding colonies as regular haulout sites where pups were absent during the breeding season, or where pup production was erratic or minimal (no more than 100 pups). Recently, breeding has occurred on a regular basis at three colonies previously classified as non-breeding colonies by Oosthuizen and David (1988), namely Cape Frio, Bird Island (Lambert's Bay) and Paternoster Rock. We considered these to be breeding colonies from the year of the first count with more than 100 pups (1993, 1986 and 1996 respectively).[2] Mercury Island is considered here to be a breeding colony for the period 1985–1990, after which seals were displaced from the island by human interference (Crawford *et al.* 1994).

Accounting for missing data in censuses

Since 1990, assessments of the size and trend of the pup population (e.g. Butterworth and Wickens 1990, Wickens *et al.* 1991, Butterworth *et al.* 1995) made use only of data from the census years in which comprehensive coverage of the pup population was attained. Such years are referred to here as 'full census' years, which we defined as a year in which two-thirds of the number of recognised breeding colonies were successfully covered. Following this criterion, there were 13 full census years between 1971 and 2004. Although census coverage in 2004 was slightly below two-thirds (65%), it was included on the grounds that the four largest colonies (Kleinsee, Cape Cross, Atlas Bay and Wolf Bay), where, on average, some two-thirds of all pups are born, were all successfully censused in this year. The remaining census years, in which counts of one or more colonies were conducted but no attempt was made to cover all or most of the population, are referred to as 'partial census' years.

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[1] In 1972, a single counter was used, and in 1977, the geometric mean rather than the arithmetic mean was used

[2] Reports (e.g. MAM pers. obs.) of increased numbers of pups born at locations not listed in the Appendix, where breeding was non-existent or sporadic during the period of this study, e.g. Vondeling Island (33°9'S, 17°58'E), Robberg (34°06'S, 23°24'E), North Reef (27°00'S, 15°19'E) and Sylvia Hill (25°08'S, 14°51'E), will only be verified once the counts of more recent censuses (2005–2007) are complete

Complete census coverage is desirable to determine the size and trend of the whole pup population. However, even in most full census years, counts from one or more breeding colonies were either lacking or were inadequate and could not be used (referred to hereafter as 'missing counts'). Reasons for this included (a) omission of a colony during a survey (e.g. for logistical reasons or owing to weather conditions), (b) incomplete coverage of one or more colonies, (c) poor-quality photographs of one or more colonies (e.g. owing to fog, photographing from too high an altitude, equipment failure or exposure of film) and (d) human disturbance to a colony prior to surveying (Shaughnessy 1987, Butterworth and Wickens 1990). For censuses to be comparable, proxy values for missing counts need to be determined. In some past studies, such values have been inferred either by using the next or previous count for the same colony or linear interpolation between the two (e.g. Butterworth *et al.* 1991, 1995, Wickens *et al.* 1991). However, considering that the pup counts at certain colonies showed considerable between-year fluctuations, especially during the latter half of the time-series (see Appendix), proxy values inferred using the above methods would be highly inaccurate in many cases. Bearing in mind that approximately two-thirds of all pups are produced at four large mainland colonies, unrealistic proxy values for these colonies could significantly influence estimates of the size and trend of the pup population or subsets of the pup population.

It follows that caution should be exercised when inferring proxy values for missing count data. Therefore, before analysing trends in the pup counts, we rigorously tested alternative approaches for estimating missing counts, with a view to finding the most robust method. This was done by simulating missing values for breeding colonies, by removing each existing count conducted in a full census year, in turn, from the time-series, and then estimating the simulated missing values (SMV) using four different approaches. For each colony, we determined the mean absolute deviations $\bar{x}$ between the existing counts (X) and the proxy counts (x) for each method apiece, such that:

$$\bar{x} = \frac{\sum_{j=1}^{J} \left| X_j - x_j \right|}{J} \qquad (1)$$

where j = each year 1,2,3,…J, for which a missing value was simulated. This measure was used to assess the accuracy of the different methods, so that a decision could be made as to how missing counts in the time-series would be determined. The following four methods were assessed.

Method 1 — nearest count

The proxy value for the SMV was taken from the nearest count of the same colony in a previous or following year. Where an SMV was midway between the previous and next counts, the arithmetic mean of the two was taken as the proxy value.

Method 2 — linear interpolation

Proxy values were determined via linear interpolation between the previous and the next existing counts of the same colony in the time-series, such that:

$$x_j = X_{jp} + \left| \frac{X_{jn} - X_{jp}}{j_n - j_p} \right| \times \left(j_j - j_p \right) \qquad (2)$$

where X is the existing count in the previous year j_p or next year j_n in which the colony was successfully censused. Where the SMVs occurred in the first or last census of the time-series, we inferred the value of the next or previous count respectively.

Method 3 — weighted mean

Both the mean and median values of all counts of a colony were tested, calculated in each case after the count to be estimated had been removed. However, it was found that a weighted mean generally gave a more accurate approximation of the existing counts. The weighted mean was calculated as follows:

$$\bar{x}_{(w)j} = \frac{\sum_{j=1}^{J} \left(X_j \times w_j \right)}{\sum \left(w_j \right)} \qquad (3)$$

such that the weights (w_j) allocated to each count declined linearly with time (years j) from the SMV, with the year furthest from the SMV assigned a weight of 1.

For the above three methods, existing counts from both full and partial census years were used when estimating proxy values for SMVs.

Method 4 — iterative imputing

Proxy values for SMVs were determined with the approach for imputing missing observations used for indices of waterbird populations in Britain (Prÿs-Jones *et al.* 1994). This method utilises an algorithm developed by Underhill and Prÿs-Jones (1994) for imputing proxy values. The algorithm is based on the view that, apart from random deviation, each proxy value can be modelled as a product of two factors, in this case a colony factor and a year factor. Simply, the procedure takes the trends in the pup counts at other colonies into account in determining proxy values. In the case of waterbird populations in Britain, Underhill and Prÿs-Jones (1994) assumed that a single model could be applied to the whole of Britain, and did not impute proxy values for missing data regionally. However, trends in abundance of Cape fur seal pups in southern Africa vary between colonies (Butterworth *et al.* 1991), and it would be inappropriate, for example, if counts of Black Rocks (Algoa Bay) were to influence imputed values at Cape Cross, considering the differences in their location and size.

With the above in mind, non-metric multidimensional scaling (MDS) (Kruskal 1964) was used to guide groupings of colonies, which were sufficiently coherent with each other that the underpinning assumption of the imputing procedure held at least approximately. Input to the MDS consisted of a similarity matrix of correlation coefficients (Pearson's r) between the time-series of all existing counts (in full and partial census years) for each colony, and all other colonies. The correlation coefficient of each pair of colonies was weighted with the least-cost swimming distance (the shortest paths through water and around land) between them, estimated using Arcview GIS (Version 3.3, Environmental Systems Research Institute, Inc.), so that both the similarity of trends in pup numbers between colonies and the distances apart of the colonies were considered. The criterion whereby groups of no less than three colonies could be subjected to the imputing process was adopted.

The proxy values were inputed step-by-step using the following algorithm:

1. Each group of associated colonies were arranged in a matrix of colony by full census year (i.e. partial census years were excluded from the matrix).
2. Each cell in the matrix that had missing data (including the relevant SMV) was replaced with an initial estimate of the missing value; the final estimate of the imputed value is not dependent on this choice. Following Underhill and Prÿs-Jones (1994), the mean of all existing counts (including from full and partial census years) were used for each colony as the initial estimate.
3. The sum of each row and each column was calculated.
4. The initial estimates of missing values with new values were replaced using the updating formula:

$$\chi_{ij}(k) = \frac{\sum_{i=1}^{I} x_{ij}(k) \times \sum_{j=1}^{J} x_{ij}(k-1)}{\sum_{i,j} x_{ij}(k-1)} \qquad (4)$$

where i is colony 1, 2, 3,…., I, j is year 1, 2, 3,…., J; and χ_{ij} is the imputed value of colony i in year j at the kth iteration (adapted from Underhill and Prÿs-Jones 1994).

5. Steps 3 and 4 were repeated until the changes between successive iterations became minimal.
6. At each iteration, if χ_{ij} of a cell that previously contained an undercount (i.e. cells flagged a–e in the Appendix) was lower than the original undercount, it was replaced with the original undercount. This was based on the rationale that, because numbers tend to be underestimated by counts, a known undercount is likely to be nearer the true number than an even lower imputed value (Underhill and Prÿs-Jones 1994).

Only breeding colonies were included in the assessment of the different methods for determining missing data, but some breeding colonies were excluded. This was on account of their growth patterns being unusual compared with most other colonies, which made it inappropriate that counts conducted at these colonies should affect imputed values at other colonies, as in the case of Method 4. The breeding colonies that were excluded were Cape Frio, Bird Island (Lambert's Bay) and Paternoster Rocks, which all became established after the commencement of the census time-series, and Mercury Island, where the trend in pup numbers was affected by management to prevent seals from displacing breeding seabirds (Crawford *et al.* 1994).

Analysis of trends in the pup population

Once values for missing data in full census years were determined, trends in pup numbers were assessed for the whole population, and subsets of the whole population (subpopulations). For the latter, the population was partitioned into countries (South Africa and Namibia), by colony type (mainland or offshore) within each country, and by geographical regions (Figure 1). Following Mecenero *et al.* (2006), Region 1 extended from the northernmost breeding colony (Cape Frio) to 24°30'S (near Meob Bay), where a biological boundary in believed to occur in the Benguela system (Agenbag and Shannon 1988). Region 2 extended from Meob Bay southward, with the southern boundary placed south of Albatross Rock (Mecenero *et al.* 2006), in the approximate vicinity of the Lüderitz Upwelling Cell, which is thought to effectively divide the Benguela into two and act as a perennial barrier to small pelagic fish prey of seals (Shannon 1985, Bianchi *et al.* 1993). Region 3 included the colonies in southern Namibia south of the Lüderitz Upwelling Cell to the Kleinsee colony in South Africa; seals from this colony forage extensively off southern Namibia (E Olsen and co-workers, Institute of Marine Research, Bergen, Norway, unpublished data). Region 4 included the remaining colonies along the west coast of South Africa, divided from Region 5 at Cape Point. Region 5 was separated from Region 6 at Cape Agulhas, based on there being a large 'dead zone' with little seal foraging activity between the colonies at Quoin Rock and Seal Island (Mossel Bay) (E Olsen and co-workers, unpublished data).

To standardise the comparisons, only the full census years were used, for the population as a whole and the various subpopulations. Trends in pup counts were assessed for the period between the first and the most recent available full census (1972–2004) and for two periods within the time-series, namely 1972–1993 and 1993–2004. These two time periods were chosen because (a) there were equal numbers of full censuses in each time period (n = 7), (b) in Namibia, where approximately 60% of the Cape fur seals' pup production occurs in most years (this study), trends in pup numbers before and after 1993 show a major discontinuity (van der Lingen *et al.* 2006), and (c) the most recent published assessment of the size and trend of the seal population (Butterworth *et al.* 1995) included records up to 1993.

Based on Caughley (1977), we determined the exponential rate of increase (r) from the slope (b) of the linear regression of the natural logarithm of pup counts on time, such that

$$r = e^{b} \qquad (5)$$

The trends in pup counts were expressed as the percentage change in numbers per year (%r):

$$\%r = \left(r - 1\right) \times 100 \qquad (6)$$

An analysis of variance (ANOVA) was used to determine whether b was significantly non-zero, accepting differences from zero occurring with less than a 5% probability ($p < 0.05$) to be significant.

Results

Comparison of methods for determining missing data

Based on the results of MDS, five groups of colonies were distinguished (Figure 2), generally dividing larger and smaller colonies within each country. The iterative imputing procedure (Method 4) was based on these groups.

The values of $\bar{x}$ (Equation 1) are given in Table 1. The performance of the different methods, in terms of their accuracy, varied between colonies. Based on this, perhaps the most accurate approach for determining proxy values for missing counts would be to alternate between methods, according to which method was the most accurate for each colony. However, we had to consider that, with additional censuses in the time-series, the accuracy of the alternative methods may change in relation to each other in future assessments. Comparing the different methods per colony is laborious and time-consuming, and it would be impracticable to repeat the process for each future assessment. From this point of view, it would be desirable to be able to apply a single method to determine proxy values for all missing counts.

However, it was evident from Table 1 that generally the accuracy of Method 4 was markedly superior to the other methods in the case of Namibian colonies, although much less so for South African colonies, where Method 2 was the most accurate. Consequently, it was decided to discard Methods 1 and 3 and use either Method 2 or 4 to determine proxy values for missing counts. The method used was based on which country a given colony occurred in, with a few exceptions which are discussed below. Results are shown in Table 2.

The growth patterns at Lion's Head and Cape Cross deviated from the remaining Namibian colonies (Figure 2), but they could not be grouped together under Method 4 owing to the criterion that groups should comprise no less than three colonies. Proxy values for missing counts at Lion's Head, the southernmost Namibian colony, were therefore estimated using Method 2, as for all South African colonies. There were no missing counts for Cape Cross in full census years.

Method 4 was used to impute the proxy values for the missing counts of the two groups of Namibian colonies distinguished in Figure 2. In the group comprising Atlas Bay, Wolf Bay, Van Reenen Bay and Long Island, Method 4 had produced relatively accurate proxy values for SMVs at the first

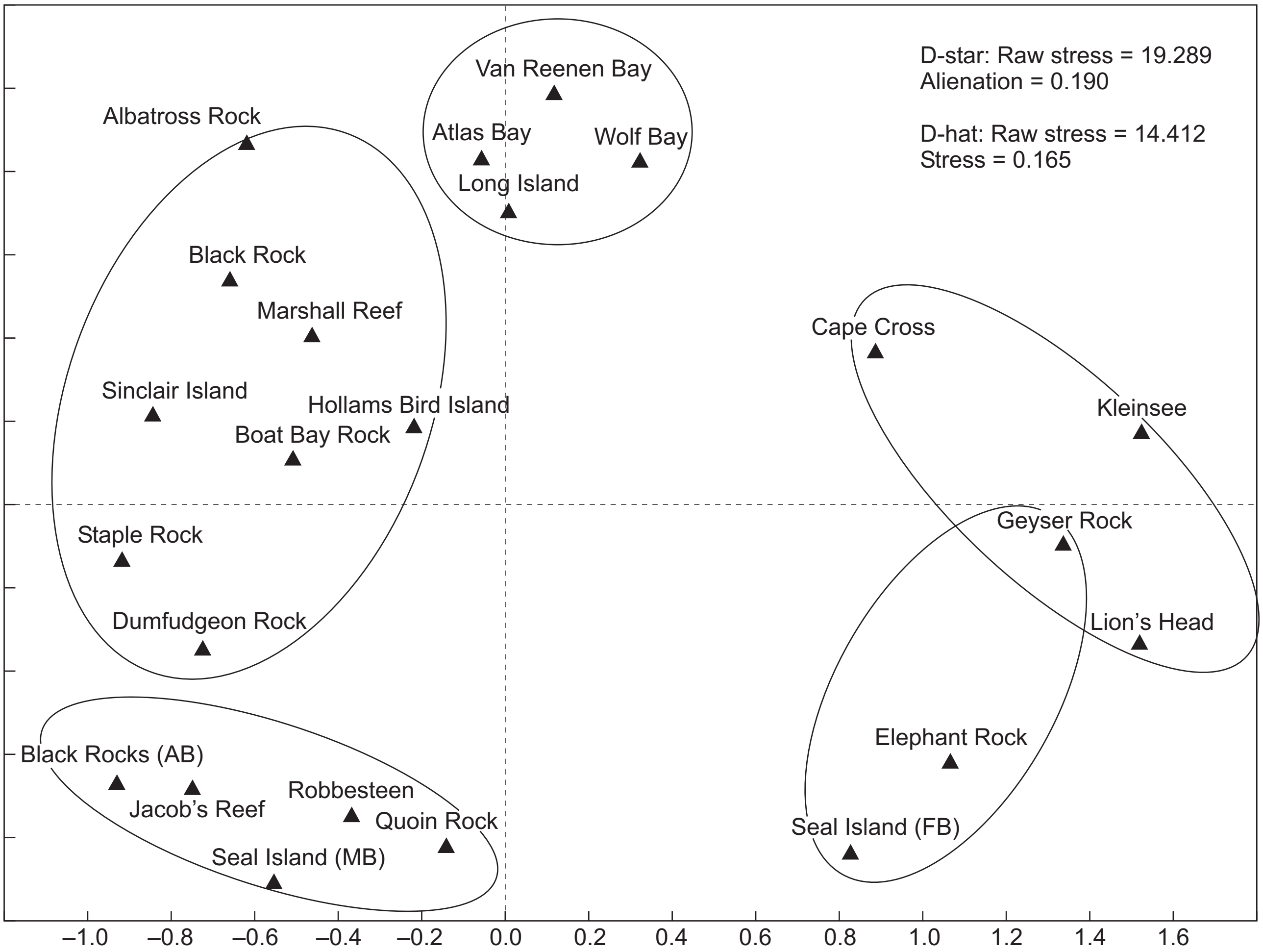

Figure 2: Two-dimensional scatter-plot produced by non-metric multidimensional scaling for the relationships between trends in counts of Cape fur seal pups at colonies in South Africa and Namibia (see text for details; AB = Algoa Bay, FB = False Bay, MB = Mossel Bay)

three colonies, but highly inaccurate values for the last colony (Table 1). In this case, the method was affected by there being many empty cells in the matrix of colony by full census year among the first three colonies in the group (including five for each of Wolf Bay and Atlas Bay), and one year (1977) in which there were no reliable counts for any of these three colonies. However, because there were no missing counts for Long Island in full census years, and thus no need to impute proxy values for this colony, we adhered to this grouping.

Trends in the pup population

Pup count totals for the whole population and subsets of the population, with missing data imputed by proxy values, are plotted against time in Figure 3. Between 1972 and 1993, pup counts of the whole population (3.1% y^{-1}), Namibia (3.3%) and South Africa (2.8%) increased significantly (Table 3). However, significant growth over this period occurred only at the mainland colonies of both countries (Namibia mainland = 4.3%; South Africa mainland = 4.1%), and at the regions in which mainland colonies occur (Region 1 = 6.9%; Region 2 = 2.8%; Region 3 = 2.8%). Pup counts at offshore colonies generally fluctuated between 1972 and 1993, and no significant change in numbers could be detected during that period.

Table 1: The mean absolute deviations $(\bar{x})$ between the existing pup counts of Cape fur seal colonies in South Africa and Namibia and the proxy counts for simulated missing values (see Equation 1), as determined using each of the four methods (1 = nearest count; 2 = linear interpolation; 3 = weighted mean; 4 = iterative imputing). The number of existing pup counts for each colony are given in parentheses. For each colony, the most accurate and the least accurate methods, in terms of $\bar{x}$, are highlighted in bold and italics respectively

	Method			
Colony	1	2	3	4
	Namibia			
Cape Cross (13)	**6 938**	7 788	*12 566*	9 083
Hollams Bird Island (11)	*1 638*	1 446	1 352	**876**
Marshall Reef (8)	230	234	*273*	**183**
Staple Rock (9)	423	*445*	403	**324**
Boat Bay Rock (10)	**244**	289	*438*	307
Dumfudgeon Rock (9)	755	*772*	702	**624**
Wolf Bay (8)	12 095	*12 626*	10 319	**4 717**
Atlas Bay (8)	18 174	*19 866*	17 466	**7 295**
Long Island (13)	3 866	**3 531**	3 826	*9 975*
Albatross Rock (11)	**961**	1 103	*1 105*	1 078
Black Rock (12)	*115*	109	93	**56**
Van Reenen Bay (11)	1 119	1 042	*1 129*	**824**
Sinclair Island (13)	2 258	2 072	**1 847**	*2 259*
Lion's Head (12)	**1 293**	1 341	*1 514*	1 460
$\Sigma\bar{x}$	50 109	52 664	*53 033*	**39 061**
	South Africa			
Kleinsee (11)	7 574	**6 166**	9 184	*14 205*
Elephant Rock (13)	807	*829*	**726**	779
Jacob's Reef (11)	1 067	**937**	1 039	*1 092*
Robbesteen (12)	*432*	**302**	369	361
Seal Island, False Bay (12)	3 000	2 711	**2 273**	*3 138*
Geyser Rock (11)	**1 374**	1 411	*2 318*	2 137
Quoin Rock (12)	394	**393**	*532*	494
Seal Island, Mossel Bay (8)	*550*	469	535	**262**
Black Rocks (10)	242	**232**	*320*	271
$\Sigma\bar{x}$	15 440	**13 450**	17 296	*22 739*
	All colonies			
$\Sigma\bar{x}$	65 549	66 114	70 329	61 800

Table 2: The proxy values for missing pup counts of Cape fur seal colonies (indicated by blocked cells in the Appendix) in South Africa and Namibia, determined using either Methods 2 or Method 4 (see text for details)

Year	Colony	Proxy value
1972	Wolf Bay	20 607
	Atlas Bay	33 092
	Black Rock	380
	Seal Island, False Bay	12 520
1977	Wolf Bay	17 423
	Atlas Bay	27 979
	Van Reenen Bay	3 240
1980	Marshall Reef	473
	Hollams Bird Island	3 308
	Wolf Bay	21 102
	Atlas Bay	33 888
	Lion's Head	2 431
	Jacob's Reef	3 452
1983	Marshall Reef	446
	Staple Rock	1 859
	Kleinsee	77 393
1986	Hollams Bird Island	2 917
	Wolf Bay	23 485
	Atlas Bay	37 714
	Albatross Rock	2 811
	Kleinsee	79 929
	Seal Island, Mossel Bay	1 102
	Black Rocks, Algoa Bay	746
1989	Seal Island, Mossel Bay	1 215
1995	Marshall Reef	277
	Staple Rock	1 154
	Boat Bay Rock	702
	Dumfudgeon Rock	785
	Seal Island, Mossel Bay	872
	Black Rocks, Algoa Bay	380
1996	Marshall Reef	307
	Staple Rock	1 280
	Boat Bay Rock	779
	Dumfudgeon Rock	871
	Seal Island, Mossel Bay	930
	Black Rocks, Algoa Bay	338
1997	Dumfudgeon Rock	891
	Wolf Bay	21 427
	Atlas Bay	34 410
2002	Jacob's Reef	2 801
	Robbesteen	990
	Geyser Rock	11 184
2004	Marshall Reef	434
	Staple Rock	1 808
	Boat Bay Rock	1 100
	Dumfudgeon Rock	1 230
	Albatross Rock	2 926
	Van Reenen Bay	5 121
	Geyser Rock	11 184
	Quoin Rock	1 223
	Seal Island, Mossel Bay	658

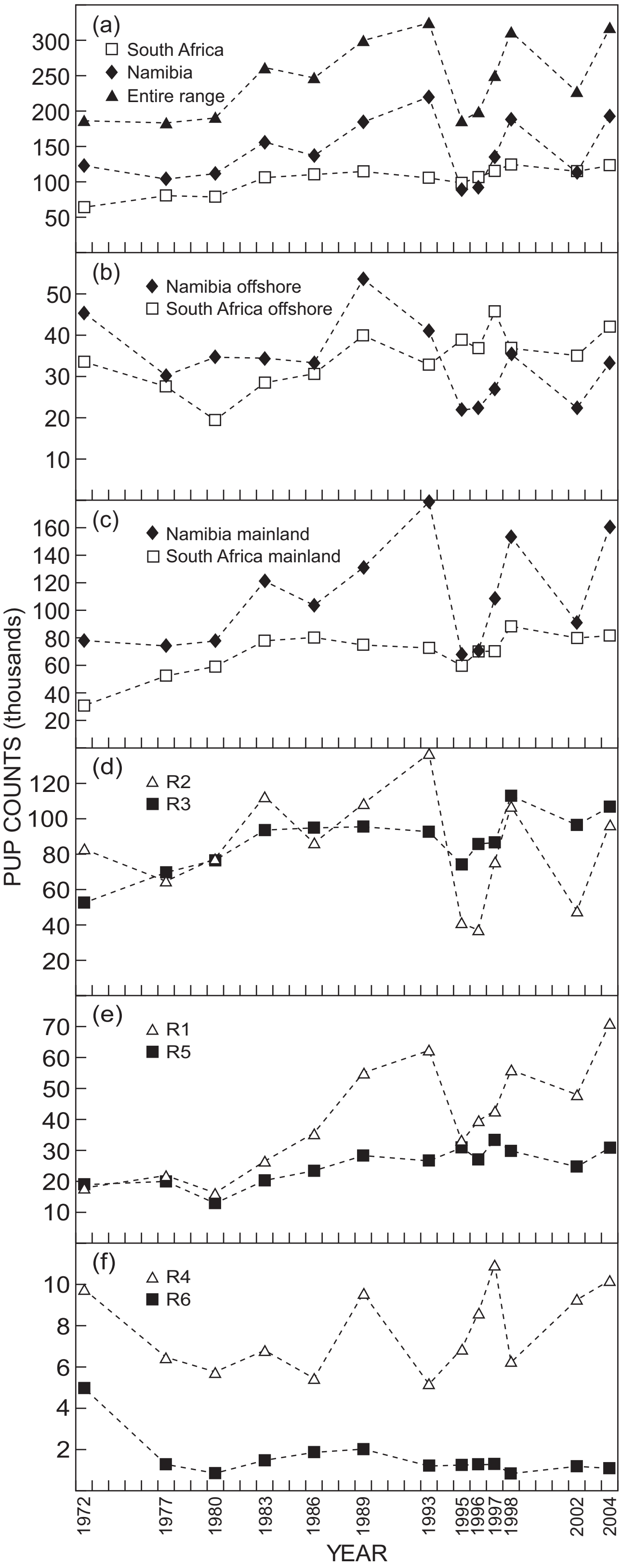

Figure 3: Trends in pup counts of Cape fur seals in South Africa and Namibia, based on aerial photographs by (a) country, (b and c) colony type (offshore or mainland) within each country and (d–f) region (R1–R6). Only counts from full census years are presented. Note the differences in scale between the y-axes

The period 1993–2004 was characterised by considerable fluctuations in pup counts (Figure 3), particularly in Namibia, which would have reduced the ability of the analysis to detect significant changes (Table 4). In most cases, the confidence intervals about the estimated percentage annual rate of change were very broad. In South Africa, the rate of increase in pup counts over this period (1.6%) bordered on significance, as did the rate of increase for Region 4 (4.7%).

Over the entire time-series (1972–2004), the rates of increase for South Africa (1.7%), mainland and offshore colonies in South Africa (2.1% and 1.5% respectively), and Region 1 (4.2%), Region 3 (1.5%) and Region 5 (2.1%), were all significant (Table 5). The rate of increase for the whole pup population (1.2%), and the rate of decline in Region 6 (–2.5%), both bordered on significance.

Discussion

Pup counts as indicators of annual pup production

Two methods have been employed in the past to estimate the numbers and trends of Cape fur seal pups, namely counts of pups on aerial photographs, and pup population size estimates from tag-recapture experiments (Shaughnessy 1987, 1993). Aerial photographic censuses of pups are the most practical means of assessing the population owing to the large number and wide geographical distribution of the colonies. Therefore, they comprise the longest and most complete time-series of pup numbers, from 1971 to the present, and have formed the basis of most assessments of the seal population's size or trend (e.g. Wickens *et al.* 1991, Butterworth *et al.* 1995). Although tag-recapture operations were considered by Shaughnessy (1993) to be the more accurate method, they are time-consuming and costly, and require a lot of manpower. Therefore, they could only be applied in a few colonies during any given year, and they were discontinued in Namibia and South Africa in 1989 and 2002 respectively (Marine and Coastal Management, unpublished data).

The opportunity to use aerial photography to record annual pup numbers is provided by the time window in which almost all the pups of the year are present in the colonies. However, counts of the pups on the aerial photographs underestimate the numbers of pups born: pups die before the aerial census, they may be born after the census, be hidden in crevices or shadows, or they may form tightly bunched crèches that are difficult to count (Shaughnessy 1987). Despite these inherent biases, Shaughnessy (1987) found the magnitude of error introduced by aerial photography to be independent of the size of colonies, and concluded that, despite being underestimates, counts from aerial photographs are useful indicators of the numbers of pups born, provided that there is consistency in the method and between counters.

Although different counters were used during the time-series, one person (MAM) oversaw the process throughout, and supervised the training of new counters. We have therefore assumed that counting over the course of the time-series has been fairly consistent. However, improvements in the quality of photographs, owing to improvements

Table 3: Linear regressions between the natural logarithms of pup counts and years, between 1972 and 1993. The percentage change in pup counts per year (%r) is given with the 95% confidence interval (CI) in parentheses. Also shown is the F statistic of the ANOVA, testing whether the slope of the linear regression was significantly non-zero

		Regression statistics				
Population	Regression	r^2	$F_{1,5}$	p	%r	95% CI
Whole population	y = 0.030x – 47.888	0.86	31.80	<0.05	3.08	(1.67 – 4.52)
Namibia	y = 0.032x – 51.759	0.73	13.33	<0.05	3.26	(0.95 – 5.62)
South Africa	y = 0.027x – 42.875	0.79	18.75	<0.05	2.78	(1.12 – 4.46)
Namibia offshore	y = 0.007x – 2.770	0.06	0.31	0.60	0.68	(−2.40 – 3.84)
Namibia mainland	y = 0.042x – 70.980	0.82	22.24	<0.05	4.25	(1.91 – 6.64)
South Africa offshore	y = 0.010x – 10.344	0.11	0.64	0.46	1.05	(−2.29 – 4.50)
South Africa mainland	y = 0.040x – 68.006	0.70	11.55	<0.05	4.07	(0.98 – 7.25)
Region 1	y = 0.067x – 122.800	0.83	24.59	<0.05	6.94	(3.29 – 10.73)
Region 2	y = 0.026x – 43.089	0.60	7.43	<0.05	2.79	(0.16 – 5.50)
Region 3	y = 0.028x – 43.413	0.79	18.39	<0.05	2.80	(1.11 – 4.51)
Region 4	y = −0.014x + 37.406	0.16	0.97	0.37	–1.43	(−5.07 – 2.35)
Region 5	y = 0.023x – 37.000	0.43	3.75	0.11	2.40	(−0.77 – 5.67)
Region 6	y = −0.032x + 70.331	0.16	0.97	0.37	−3.12	(–10.81 – 5.23)

Table 4: Linear regressions between the natural logarithms of pup counts and years, between 1993 and 2004. The percentage change in pup counts per year (%r) is given with the 95% confidence interval (CI) in parentheses. Also shown is the F statistic of the ANOVA, testing whether the slope of the linear regression was significantly non-zero

		Regression statistics				
Population	Regression	r^2	$F_{1,5}$	p	%r	95% CI
Whole population	y = 0.012x – 11.102	0.04	0.21	0.67	1.19	(−5.32 – 8.13)
Namibia	y = 0.012x – 11.237	0.01	0.08	0.79	1.16	(−9.21 – 12.71)
South Africa	y = 0.016x – 19.929	0.50	5.06	0.07	1.59	(−0.23 – 3.44)
Namibia offshore	y = −0.006x + 22.420	0.01	0.04	0.84	−0.61	(−7.81 – 7.16)
Namibia mainland	y = 0.016x – 20.606	0.02	0.13	0.74	1.63	(−9.60 – 14.24)
South Africa offshore	y = 0.0090x – 7.234	0.10	0.56	0.49	0.89	(−2.15 – 4.03)
South Africa mainland	y = 0.020x – 28.132	0.36	2.77	0.16	1.99	(−1.06 – 5.14)
Region 1	y = 0.030x – 48.589	0.19	1.14	0.33	3.02	(−4.09 – 10.65)
Region 2	y = −0.001x + 13.590	0.00	0.00	0.98	−0.12	(−14.14 – 16.18)
Region 3	y = 0.021x – 30.053	0.33	2.43	0.18	2.10	(–1.34 – 5.66)
Region 4	y = 0.046x – 83.253	0.43	3.71	0.11	4.73	(–1.53 – 11.38)
Region 5	y = −0.000x + 11.003	0.00	0.00	0.98	−0.04	(−3.07 – 3.10)
Region 6	y = −0.013x + 32.809	0.11	0.60	0.47	–1.28	(–5.40 – 3.02)

Table 5: Linear regressions between the natural logarithms of pup counts and years, between 1972 and 2004. The percentage change in pup counts per year (%r) is given with the upper and lower 95% confidence interval (CI) in parentheses. Also shown is the F statistic of the ANOVA, testing whether the slope of the linear regression was significantly non-zero

		Regression statistics				
Population	Regression	r^2	$F_{1,5}$	p	%r	95% CI
Whole population	y = 0.015x – 10.457	0.27	4.02	0.07	1.16	(−0.11 – 2.44)
Namibia	y = 0.007x – 2.145	0.06	0.65	0.44	0.70	(−1.21 – 2.66)
South Africa	y = 0.017x – 22.410	0.73	29.02	<0.05	1.72	(1.01 – 2.43)
Namibia offshore	y = –0.013x + 35.700	0.21	2.96	0.11	–1.26	(−2.86 – 0.36)
Namibia mainland	y = 0.014x – 15.980	0.17	2.19	0.17	1.39	(−0.67 – 3.50)
South Africa offshore	y = 0.014x – 18.286	0.42	8.05	<0.05	1.45	(0.32 – 2.60)
South Africa mainland	y = 0.020x – 29.221	0.52	12.09	<0.05	2.05	(0.75 – 3.36)
Region 1	y = 0.041x – 70.766	0.72	28.81	<0.05	4.17	(2.44 – 5.93)
Region 2	y = −0.007x + 25.263	0.03	0.34	0.57	−0.70	(−3.31 – 1.98)
Region 3	y = 0.015x – 18.414	0.54	13.16	<0.05	1.51	(0.59 – 2.43)
Region 4	y = 0.007x – 5.854	0.08	0.97	0.35	0.75	(−0.91 – 2.43)
Region 5	y = 0.020x – 30.426	0.59	15.82	<0.05	2.06	(0.91 – 3.21)
Region 6	y = −0.025x + 57.685	0.30	4.76	0.05	−2.50	(−4.97 – 0.02)

in censusing equipment and methods, would have resulted in greater accuracy of counts, and would likely increase estimates of the rates of change in pup numbers over time. Butterworth *et al*. (1995) found that a switch from flying with a fixed-wing aircraft to a helicopter, when censusing most of the South African colonies, did not seriously compromise the compatibility of counts. More recently, there has been a switch from black and white film to colour digital photography. This occurred in 2006 and therefore does not affect the present study (up to 2004). For future assessments, the effects of using different photographic technology must be taken into consideration in seal counts.

Accounting for gaps in the pup count time-series

Where pup counts of colonies are used collectively to determine rates of change for the whole pup population or subsets of it, it is necessary to determine values for counts of colonies that are missing in any years. In Butterworth *et al.* (1987) and Butterworth and Wickens (1990), missing counts at colonies were estimated from separate linear models of the log-transformed counts available for each colony. In this way, values for each colony were estimated for every year in the time-series, and pup numbers for the whole population in each year were calculated by summing the values for all the colonies. This approach was rejected after it became apparent that fluctuations in pup counts between years resulted in poor fits of the models to the available count data of many colonies (Butterworth *et al.* 1991).

A simpler method was subsequently adopted (Butterworth *et al.* 1991, 1995, Wickens *et al.* 1991), whereby only the years with comprehensive surveys (full census years) were used to model the pup census values of the population as a whole. The same approach was used to determine pup numbers and trends in this study. This still requires that inferences be made for gaps in the data in full census years, because using only the totals of the available counts can give a misleading impression of the population trend, particularly when counts for large colonies are missing in a year. In the aforementioned studies, gaps in the count data were filled using linear interpolation between the previous and the next counts of the same colony, or by inferring the same value as a neighbouring count in the time-series for the same colony.

Inspection of the time-series (see Appendix) shows that neither approach is always satisfactory. For example, estimating proxy values in place of the existing 1998 counts at Wolf Bay and Atlas Bay from the 1996 and 2002 counts of these colonies results in underestimates of the existing count by about 70%. It follows that either approach would have caused the 1998 pup count for the Namibian seal population, and for the whole seal population, to be underestimated by about 30% and 20% respectively.

Following comparison of the accuracy shown by each of four alternative methods in approximating the correct values of available counts, two methods were chosen, one relevant to South African colonies and the other to most Namibian colonies. The reasons for this approach can be explained as follows: (a) in general, the pup counts of Namibian colonies were far more variable between years than those of South African colonies, so linear interpolation (Method 2) was inappropriate for most Namibian colonies; and (b) there was generally greater similarity between the trends in pup counts of Namibian colonies than there was between South African colonies. This is evident in the MDS scatter-plot (Figure 2), where dissimilarities between South African colonies were most pronounced in the primary dimension, as opposed to Namibian colonies (with the exception of Lion's Head). Therefore the iterative imputing algorithm (Method 4), which in imputing proxy values takes into account the patterns at other colonies within each colony's MDS group, was better suited to Namibian than South African colonies. Causes of these general differences in the pup count trends of colonies between the two countries are discussed later.

With regard to future assessments, each additional census will influence imputed proxy values throughout the time-series, and therefore affect the estimated totals of all census years (Underhill and Prÿs-Jones 1994). Such changes should be relatively small, but, partly for this reason, it is advisable to have as few missing values that require imputation as possible, and the systematic design of censusing to omit colonies or even years in the knowledge that values can be imputed should be avoided. Where additional censuses cause large changes in imputed values, it would be advisable to re-assess the regional groupings of colonies, through application of the MDS model. In the case of colonies for which the linear interpolation method is used, only the proxy values for missing counts at the end of the time-series would have to be adjusted when additional counts become available.

The 1972 census was the first full census, and is therefore the 'anchor' year of the time-series. This census has been acknowledged to be less reliable than subsequent full censuses, because certain errors have become apparent (Shaughnessy 1987). Most significantly, the number of pups harvested at the Wolf Bay and Atlas Bay colonies (c. 42 200 combined) was substantially higher than the pup counts at these colonies (c. 16 300), probably on account of incomplete aerial coverage (Shaughnessy 1987). Wickens *et al*. (1991) and Butterworth *et al*. (1995) replaced the original counts with the next available reliable counts in the time-series for these two colonies. Given the harvest returns, this proxy value (c. 54 300 combined) was considered by Wickens *et al*. (1991) not to be unrealistic, assuming a low mortality rate between the census and harvesting in that year. This value is very similar to the value of c. 53 700 imputed here for Wolf Bay and Atlas Bay combined. As these were the only large colonies for which it was necessary to determine proxy values in 1972, the total count for that year is very similar to our values and those of other studies.

The 1986 full census has been omitted from some previous assessments of the seal population (e.g. Wickens and Butterworth 1990, Wickens *et al*. 1991), on the grounds that bull harvesting, which was allowed in Kleinsee, Atlas Bay and Wolf Bay at the time, extended well into the pupping season and caused disturbance. Consequently, the low counts for these colonies (see Appendix) were considered to be non-representative of the numbers born there in 1986.

Here, we determined proxy values for these three colonies for 1986 (Table 2), which in the case of the two Namibian colonies were lower than the existing counts of the preceding and succeeding censuses (Appendix). Correspondingly, the total pup counts for Namibia and for the whole population were relatively low (Figure 3a). We considered this to be realistic, given that environmental conditions in the northern Benguela in 1984–1985 are known to have decreased the productivity of the system and depleted the stock sizes of several of the seals' prey species (Roux 2003), and may therefore have impacted on the birth rate of the seal population (discussed later).

Interpreting the trends in pup numbers

Censuses of pup numbers have frequently been used as indicators of the overall size of seal populations, assuming some fixed ratio between pup numbers and older age-classes in the population (e.g. Pistorius *et al*. 1999, Kirkwood *et al*. 2005). A factor of 4.0 (David 1987), later revised to 4.8 after more accurate information became available (Butterworth *et al.* 1988), has been employed to estimate the size of the Cape fur seal population size from pup census results. However, Wickens and Shelton (1992) showed that trends between pup numbers and the seal population size can differ as a result of variability in life history parameters (e.g. survival rates, pregnancy rates) and harvesting of pups and bulls. Thus, caution needs to be used in inferring seal population numbers and trends directly from pup counts. The considerable fluctuations in pup counts that occurred between 1993 and 2004, particularly in Namibia, are a case in point (Figure 3a). The reduced pup counts in the census years between 1993 and 1998, and again between 1998 and 2004, were associated with unfavourable environmental/feeding conditions in the northern Benguela during 1994–1995 and again in 2000–2001, which caused the starvation and deaths of tens of thousands of seals (pups and older animals) in Namibia (Roux 1998, Roux *et al.* 2002). Prey shortages also impact negatively upon birth rates of seals (Guinet *et al.* 1998), and the years of unfavourable feeding conditions were marked by a high incidence of abortions at many Namibian colonies during winter (Roux 1998, 2002). Given that pup counts had recovered rapidly by the time of the 1998 and 2004 censuses, to numbers comparable to the census before each downward flux, it is probable that reduced birth rates of adult females (e.g. because of failure to come into oestrus, failure to implant or failed pregnancies), rather than adult female mortality, were mainly responsible for the reduced pup counts in Namibia in 1995–1997 and 2002. Multiplying the number of pup births by a constant factor to estimate the numbers of seals in older age-classes would have resulted in a considerable underestimation of the Namibian and overall seal population sizes in years affected by low birth rates.

A better method of assessing the size of the seal population, than simply inferring it annually from pup counts, is to model the population based on demographic parameters and long-term trends in pup numbers (Wickens and Shelton 1992). Butterworth *et al.* (1995) estimated the seal population (South Africa and Namibia) for 1993 at about two million individuals (including pups). In the present study, the considerable variability in pup counts between years, together with the shortness of the time-series, reduces the ability of the statistical analysis to detect significant changes in pup numbers during 1993–2004. This applies to the whole population and some of the subpopulations defined in this study (particularly in Namibia). However, if it is assumed that the birth rates of the whole population in 1993, 1998 and 2004 (the only three census years in the latter time period with comparatively high pup counts) were similar, it appears that the seal population has stabilised at around its 1993 level, based on the pup counts (Figure 3a). This is contrary to the prediction that the seal population would double between 1990 and 2000, assuming conditions of no further harvesting after 1990, and an absence of density dependent effects on the population (Butterworth and Wickens 1990, Butterworth *et al.* 1991). Effects of continued harvesting in Namibia may have contributed to the decline in the growth rate of the population. However, circumstances (discussed below) support the view that the main cause of the reduced rate of increase during 1993–2004 compared with 1972–1993 (Tables 3, 4) is the effect of reduced prey availability on the carrying capacity of the population.

The environmental perturbations that occurred in the northern Benguela between 1993 and 1995 caused large declines of fish stocks as a result of death, migration and poor recruitment. These events included an extended low-oxygen event affecting shelf waters off Namibia, and a severe Benguela Niño event that caused a warm-water intrusion onto the Namibian shelf (Gammelsrød *et al.* 1998). It is believed that continued high levels of fishing during these unfavourable periods exacerbated the effects on some fish stocks (Boyer and Hampton 2001). The biomass levels of marine biota (including prey species of seals) in the northern Benguela have not yet recovered to their previous levels (Cury and Shannon 2004), despite reduced fishing pressure there since 2000 (van der Lingen *et al*. 2006). This has been interpreted as an indication of a 'regime shift' in the ecosystem, and it is considered unlikely that a recovery will occur within a short time period (Cury and Shannon 2004). The productivity of other top predators besides seals in the northern Benguela also appear to have been affected by the reduced availability of prey. These include seabirds such as the African penguin *Spheniscus demersus* and Cape gannet *Morus capensis* (Crawford *et al.* 1995, Kemper 2006).

In Namibia, it is noteworthy that, whereas Region 2 accounted for 62% of Namibia's pup numbers in 1993, it accounted for 56% and 50% in 1998 and 2004 respectively. Correspondingly, Region 1 accounted for 28%, 30% and 37% of Namibia's pups. The pup counts in Region 3 (which also includes Kleinsee in South Africa) increased by 22% from 1993 to 1998. Given the rapid rate of growth in pup numbers at Cape Frio (Figure 1) in Region 1, migration of adults appears to have played an important role in the changing distribution of the population in Namibia. Cape Frio was described as a non-breeding colony by Oosthuizen and David (1988); pup counts between 1993 and 2004 increased at about 30% per annum (95% CI 11–52%,

$F_{1,5} = 19.13$, $p < 0.05$; see Appendix). This rate could only have been sustained by immigration, because the maximum intrinsic rate of increase of a fur seal colony is about 13% per annum (Wade 2002).

The distributional shifts in the seal population in Namibia are likely in response to shifts in the geographical distribution of prey (van der Lingen *et al.* 2006). This is supported by the fact that the decline in Region 2 was not confined to the mainland sites of Wolf and Atlas bays, as would be expected if effects of harvesting were driving the changes, but was also evident at offshore locations. Harvesting activity in Region 2 was restricted to these two mainland sites throughout 1993–2004; at these sites pup counts in 1998 and 2004 were 81% and 73% of their 1993 level respectively. The corresponding counts at offshore colonies in Region 2, where no harvesting took place, were 71% and 65% of their 1993 level, suggesting a common cause for the declines on both the mainland and the islands — probably prey availability.

In 1984, another severe Benguela Niño event had occurred in the northern Benguela, which severely affected several fish stocks (Roux 2003). No census coincided with the occurrence of the event, but the relatively low pup count for Namibia (and the whole population) in 1986 may reflect a reduced birth rate influenced by this event. The breeding populations of Cape gannets, African penguins and bank cormorants *Phalacrocorax neglectus* in Namibia were also reduced at this time, compared with preceding and succeeding censuses (Crawford *et al*. 1995, 1999, van der Lingen *et al*. 2006).

The seal population has been considerably more stable off South Africa than off Namibia between 1972 and 2004. This suggests that the southern Benguela has not been subjected to environmental perturbations of the same strength or effect as the northern Benguela over that period. Also, fish stocks appear to have benefited from relatively conservative fisheries management strategies implemented by South Africa over the past several decades (Cury and Shannon 2004). Nevertheless, there have been recent shifts in the geographical distribution of important pelagic prey species in the southern Benguela, most importantly, the eastward shift in the distribution of the sardine *Sardinops sagax* stock since 2001 (van der Lingen *et al.* 2005, 2006). However, whereas changes in the geographical distribution and abundance of prey in the northern Benguela have apparently influenced large-scale distributional shifts in Namibia's seal breeding population (see above), there is much less scope for the breeding population to track the spatial shifts in prey availability taking place in the southern Benguela. South of Kleinsee (Figure 1), the colony where the bulk of South Africa's seal population breeds, nearly all the recognised seal breeding colonies occur on small offshore locations (≤2.2ha, Rand 1972), offering little or no space for further growth of existing colonies. Up to now, seal colonies have been prevented from re-establishing at most of the larger islands off South Africa from where seals were previously eradicated (Shaughnessy 1984). Moreover, there is little scope for breeding colonies to establish themselves on the mainland along the south-west or south coasts of South Africa (Regions 4–6), because the potential for human interference is much greater than in the largely restricted or reserved coastlines of Namibia and the Northern Cape province (Stewardson 1999). Therefore, the combination of limited breeding space and spatial shifts in the availability of prey in the southern Benguela may have contributed to the perceived stabilisation in growth of South Africa's population during 1993–2004 compared with 1972–1993 (Tables 3, 4).

Nevertheless, pup counts for the offshore colonies in South Africa, and for Region 5 which consists of offshore colonies, increased significantly from 1972 to 2004 (Table 5). The establishment and growth of breeding colonies at Paternoster Rocks and Bird Island in Lambert's Bay (Figure 1) since the late 1980s explains some of the perceived growth at offshore colonies, although not for Region 5. Early in the census time-series, Shaughnessy (1987) described the Quoin Rock and Elephant Rock colonies as being well below their carrying capacities as a result of over-harvesting of pups. Pup harvesting figures reported by Wickens *et al*. (1991) show a similar situation for Geyser Rock and Seal Island (Mossel Bay). After adjusting the pup counts in the Appendix upwards to compensate for undercounting[3] and pup mortality[4], it is calculated that harvest rates at these two colonies were on occasions as high as 63% (1972) and 100% (1975) respectively of the pups born there. This is despite the fact that the harvesting rate recommended for a maximum sustainable yield was estimated to be between 30% and 35% of pups available (Shaughnessy and Best 1982). Therefore, with the cessation of pup harvesting at the island colonies in the late 1970s and early 1980s, the higher pup counts in subsequent censuses, at least at the above four locations (see Appendix), probably resulted from compensatory growth. This would have had a positive effect on the trends in pup counts over the entire times-series.

In summary, numbers increased significantly from 1972 to 1993, both in Namibia and South Africa, with mainland colonies accountable for most of the growth. Significant changes could not be detected for the period 1993–2004, owing to considerable year-to-year variability between pup counts, especially in Namibia. However, based on the pup counts in years that were apparently 'favourable' for pup production, there appears to have been little change in the overall population size since 1993, when it was estimated at about two million animals.

Acknowledgements — SPK was funded by the Benguela Current Large Marine Ecosystem (BCLME) project 'A Regional Ecosystem Monitoring Programme: Top Predators as Indicators of Ecosystem Change in the BCLME' (LMR/EAF/03/02). LGU acknowledges support from the Sea and Coast II Programme of the National Research Foundation, the University of Cape Town Research Committee, and the Earthwatch Institute. We thank Jeremy David, Greg Hofmeyr, Dave de Villiers, Stefan Swan and Dandelene Reynolds for their assistance with the aerial censuses and counts, and Laurent Drapeau for his assistance with GIS. The aerial censuses were financed and orchestrated by

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[3] A factor of 1.05, estimated to scale pup counts to tag-recapture estimates of pup numbers at island colonies (Butterworth *et al.* 1991)

[4] A factor of 1.18, based on the average rate of pup mortality between birth and mid-December at the Atlas Bay colony, between 1988 and 2002 (Johnston and Butterworth 2004)

South Africa's Department of Environmental Affairs and Tourism (branch Marine and Coastal Management), with logistical and partial financial support from Namibia's Ministry of Fisheries and Marine Resources. The valuable suggestions and comments from Peter Shaughnessy and an anonymous reviewer on an earlier version of the manuscript are greatly appreciated.

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Manuscript received January 2007; accepted April 2007

Appendix: Pup counts from aerial surveys (1971–2004). The years underlined were full census years, and blocked cells indicate missing or inadequate counts for which proxy values were determined in this study. In all other blank cells, counts were not made. Included are data previously presented in Shaughnessy (1987), Oosthuizen and David (1988), Wickens *et al.* (1991), Butterworth *et al.* (1995) and results of more recent surveys

Colony	1971	1972*	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987
Cape Frio		0							0				1			3	
Cape Cross		17 839					22 097			16 327			26 623			35 590	
Hollams Bird Island		5 042					2 772						1 945				
Mercury Island		0					0			0			0		1 128	3 606	3 828
Marshall Reef		755					378	258								398	
Staple Rock		2 910					2 114	2 472		1 236						2 212	
Boat Bay Rock		1 691					978	971		528			1 167			1 618	
Dumfudgeon Rock		2 875					779	920		616			883			1 623	
Wolf Bay		7 443[b]		8 805[a]			15 017[b]		17 852				26 669			10 616[c]	
Atlas Bay		8 879[b]		23 295[a]			23 759[b]	36 453	55 852				61 438			16 860[c]	
Long Island		12 228					9 840		13 361	12 252			13 223			12 812	
Albatross Rock		3 722					2 393			4 632			5 254				3 331
Black Rock							205			278			216		407	202	393
Van Reenen Bay		3 243					3 208[a]			3 591			4 953		6 701	4 820	6 900
Sinclair Island		15 772					10 879	9 461		11 370			9 419			8 011	
Lion's Head		2 769					3 248						1 614		1 792	1 817	
Kleinsee		30 450	27 776				52 075			59 165				83 469		43 267[c]	47 113[c]
Elephant Rock		2 496	1 095			1 629	1 398			1 826			2 748			2 612	
Bird Island, Lambert's Bay															0	10	8
Paternoster Rock																127	74
Jacob's Reef		4 808	3 376				3 772						3 132		3 270	1 086	
Robbesteen		2 427					1 273			473			929		1 515	1 616	1 368
Seal Island, False Bay	14 449[a]						12 199	12 297		8 188		8 574	10 017		11 010	12 116	5 218[d]
Geyser Rock		2 680				4 952	6 638			4 099		6 137	9 151	6 954	8 345	9 584	8 643
Quoin Rock		3 746			1 730		1 090	765		630			1 074			1 644	1 496
Seal Island, Mossel Bay		3 237			1 262		1 176	957		380			899				1 170
Black Rocks, Algoa Bay		1 703			904		86			442			561				808

Appendix (cont.)

Colony	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004
Cape Frio						477		3 044	4 337	4 419	7 191				10 880		16 608
Cape Cross	37 882	55 247	51 890	44 636	65 557	61 891		29 990	35 498	38 564	48 993				37 394		54 546
Hollams Bird Island		5 216	3 267			4 902		961	2 026	1 827	3 478				2 285		2 305
Mercury Island	5 178	3 114	460[d]			35		0	0	0	0				0		0
Marshall Reef		666		384		942				242	146				106		
Staple Rock		2 325		2 314		1 405				1 542	1 899				1 462		
Boat Bay Rock		2 066				1 240				693	883				669		
Dumfudgeon Rock		2 003		552		1 667					465				1 099		
Wolf Bay	29 454	24 548	19 286		25 680	39 534	28 476	9 642	9 158		36 700				15 184		29 531
Atlas Bay	43 923	42 223	41 607			62 823		17 031	13 581		46 225				18 193		45 155
Long Island		22 160				20 170		8 809	7 751	12 098	14 835				7 822		12 648
Albatross Rock		4 354				1 715		2 031	1 152	2 451	2 785				1 335		
Black Rock	491	439		461		200		252	210	100	206				84		259
Van Reenen Bay	6 235	5 590	4 990	5 232		5 293		3 011	3 317	3 989	5 783				2 953		
Sinclair Island		11 139				8 703		6 992	7 967	7 186	10 771				7 472		10 543
Lion’s Head		3 437				6 121		4 501	4 623	5 529	8 308				6 163		9 603
Kleinsee	46 850[c]	74 620	78 809	63 246	79 301	72 203		59 370	69 669	69 930	87 841			91 641	79 710		80 897
Elephant Rock	3 740	3 326		3 476	3 841	2 193	3 813	2 110	3 092	4 074	2 165				4 293		4 398
Bird Island, Lambert’s Bay	8	0	3	7	0	14		66	352	314	40				130		592
Paternoster Rock	943	1 098	1 527	1 697	1 877	758		2 476	1 932	3 233	1 200				1 014		908
Jacob’s Reef	1 971	3 886			3 606	1 265		1 566	2 221	2 064	1 650						3 376
Robbesteen	1 575	1 224		1 487	1 722	964		707	976	1 212	1 155						908
Seal Island, False Bay	14 105	13 503	15 484	13 898	17 522	12 974	15 235	17 144	13 528	19 396	16 806				12 298		18 339
Geyser Rock	10 187	12 793	10 749	9 651	11 522	11 743	10 324	11 616	11 939	12 266	11 184				5 659[e]		
Quoin Rock	1 756	2 041	1 676		2 367	1 834	1 694	2 080	1 520	1 639	1 779				1 223		
Seal Island, Mossel Bay			1 238			754				989	691				658		
Black Rocks, Algoa Bay		800				463				296	142				505		423

* 1972 photographs taken on 4–6 December, therefore values are adjusted by factor of 1.5539

[a] Considered undercounts because the photographs were taken in January (Shaughnessy 1987)

[b] Considered undercounts because unrealistic in comparison with harvest figures (possibly owing to incomplete coverage of colonies)

[c] Aerial surveys preceded by large bull harvests that resulted in breeding disturbance, thereby probably reducing pup production (Wickens *et al*. 1991)

[d] Breeding population deliberately disturbed during breeding season, therefore pup production reduced (Wickens *et al*. 1991)

[e] Considered undercount owing to high altitude of photographs