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Spatio-temporal shifts of the dynamic Cape fur seal population in southern Africa, based on aerial censuses (1972–2009)

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ABSTRACT

A time series of aerial censuses of Cape fur seal colonies, spanning four decades (1972–2009) and three countries (South Africa, Namibia, and Angola), was analyzed to assess spatio-temporal changes in population numbers. A weighted quantile regression approach was used to estimate trends in pup counts that were used as proxies for numbers of older animals at breeding colonies. There was a 74% increase in the number of breeding colonies over the study period, from 23 in 1973 to 40 in 2009. There was also a significant northward shift in the distribution of the breeding population. This was largely attributable to events in the northern part of the population's range coinciding with Namibia, where seal numbers declined at most colonies in the south of Namibia while several new breeding colonies developed in the northern part of Namibia and one in southern Angola. Despite range expansion and the development of new colonies, the overall size of the population in 2009 was similar to that of the early 1990s, according to the pup count models. Potential mechanisms for the observed changes, and their management implications, are discussed.

Key words: *Arctocephalus pusillus pusillus*, Angola, Benguela, model, Namibia, otariid, pinniped, South Africa, regression, trend.

Breeding colonies of the Cape fur seal, *Arctocephalus pusillus pusillus*, occur at numerous island and mainland locations situated along the south and west coasts of southern Africa (Kirkman *et al.* 2007). Prior to the 16th century, breeding colonies may have been restricted to offshore islands, due to a prevalence of mainland

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predators, including humans (Rand 1972). However, uncontrolled seal harvesting (sealing) that took place from the 16th to the 19th centuries led to the extirpation of colonies at numerous islands (Rand 1952, 1972; Shaughnessy 1984). For several decades, many of these islands were managed for the production of seabird products (especially guano) to the exclusion of seals; therefore recolonization could not occur (Rand 1963*a*, *b*). Around the middle of the 20th century breeding colonies were established at mainland locations, including Kleinsee in South Africa and Atlas Bay and Wolf Bay in Namibia (Rand 1972). These colonies and Cape Cross, a mainland colony in Namibia which existed before the 20th century, accounted for most of the growth in the seal population reported during the 20th century (Butterworth *et al.* 1995).

Since the initiation of a long term program in the early 1970s to monitor spatio-temporal trends in seal abundance by way of aerial photographic censuses (Shaughnessy 1987), there have been changes in the population's environment and in its management. Sealing ceased in South Africa in 1990, although it is ongoing in Namibia. There, it was discontinued at several island locations in the 1970s and 1980s (Wickens *et al.* 1991) and is currently practiced at three mainland colonies (Kirkman and Lavigne 2010). Human occupation of several "guano islands" ceased, opening them up to potential recolonization by seals (Shaughnessy 1984). In addition, there were substantial changes in the distribution and abundance of some of the important prey species of Cape fur seals since the 1970s (van der Lingen *et al.* 2006). It has been speculated whether such developments would impact the distribution of the seal population (Shaughnessy 1984, Kirkman *et al.* 2007).

Changes in the distribution and size of the population are of interests to managers, scientists and interested stakeholders (fishermen, conservation groups and others), especially considering the number of well-documented management issues concerning seals. These include seal-fishery interactions (Shaughnessy 1985, Wickens *et al.* 1992, Mecenero *et al.* 2007), effects of seals on the conservation status of several seabird species that are endemic to the region (David *et al.* 2003, du Toit *et al.* 2004, Makhado *et al.* 2006) and commercial harvesting of seals in a part of their range (Wickens *et al.* 1991, Kirkman and Lavigne 2010). The main aims of this study were to report on changes in the spatial distribution of the seal breeding population, including the development of new breeding colonies, especially for the period when aerial photographs were taken. To assess these distributional shifts properly required that abundance was also taken into account. Therefore numerical trends at breeding colonies were investigated, using pup numbers as a proxy. Finally, breeding colonies were aggregated to assess trends in the population at the scale of the entire region or for subsets of the population (areas).

METHODS

Aerial Censuses

From the early 1970s until 2009, aerial censuses of Cape fur seal colonies were conducted at intervals of 1–5 yr throughout the breeding range of the population. Aerial photographs were taken of the breeding colonies and used to assess the numbers of new born pups in the colonies (Kirkman *et al.* 2007). The rationale for focusing on pups at the breeding colonies, details on equipment and techniques used for aerial photography and counting of seals, including limitations and assumptions, are given in Kirkman *et al.* (2007). During most censuses, the coastline was scanned for the formation of new seal colonies in remote areas and existing "nonbreeding" colonies were checked for the presence of pups. Censuses were referred to as comprehensive censuses when at least two-thirds of known colonies were covered, or partial censuses when a smaller percentage of colonies were covered, following Kirkman *et al.* (2007).

The initial comprehensive census which took place in 1971 was disregarded in this study. This was because the timing of that census was two weeks early compared with the remainder of the time series. Only census results from 1972 (a partial census year) onwards were considered. In 2005 the mode of photography used during censuses was converted from black and white monochrome film to digital color photography. To ensure consistency in the time series of counts, all counts conducted on digital images were multiplied by an adjustment factor of 1.08 that was determined from comparison of pup counts on black and white and digital images taken of the same areas during dual censuses.[2]

Breeding and Nonbreeding Colonies

At the time when aerial censuses of seal colonies commenced in the early 1970s, 23 breeding colonies were reported (Shaughnessy 1987). A Cape fur seal breeding colony was defined by Oosthuizen and David (1988) as any location where more than 100 pups per year were counted on a regular basis. They defined a nonbreeding colony as any location where an aggregation of seals regularly occurred but where no pups were observed, or where pup counts were less than *ca.* 100. The use of this definition was continued in this study for convenient comparison with past studies and for lack of a suitable alternative. The predictions of a weighted quantile regression model through the time series of counts for each colony were used to classify the breeding status of colonies in any given year (*i.e.*, according to whether the prediction was above or below 100). This approach mitigated for effects of between year variability of pup counts on the classification of colonies, in particular colonies that had counts on either side of the 100 pup level during the time series or that fluctuated considerably in pup numbers, by attaching less weight to anomalously low counts in the time series. This model is explained below.

Rates of Numerical Change at Colonies

Trends in pup production for the 23 breeding colonies that existed at the start of the aerial census time series in 1972, and at other colonies where breeding was initiated subsequently, were assessed. For convenience, these two sets of colonies were referred to throughout as "established" and "new" colonies, respectively. Note that some of the new breeding colonies have formed at locations of extinct seal colonies, and that some of the established colonies occur at sites where seal breeding colonies were absent historically (*e.g.,* certain mainland colonies).

Assessing trends in pup counts at Cape fur seal colonies was problematical because of the variable pattern in pup counts between years, especially since the early 1990s (*e.g.,* Kirkman *et al.* 2007). It was likely that anomalously small pup counts that occurred in some years at many colonies were caused by a combination of one or more factors: mortality of new born pups prior to the aerial census (de Villiers and Roux

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[2] Unpublished data from Mdu Seakamela, Department of Environmental Affairs, Branch Oceans and Coasts, Private Bag x2, Roggebaai 8012, Cape Town, January 2010.

1992, Hofmeyr *et al.* 2011), a large proportion of pregnancies being aborted prior to the pupping season (Roux 1998) or the effects of human disturbance (Wickens *et al.* 1991). Such "outlier" counts are not necessarily useful indicators of the population of breeding-age females and in a conventional trend analysis, these small values drag the trend line away from the true level, reducing the explanatory powers of growth trends and generating smaller predictions. What was required to address this problem was an analysis tool which objectively constructed a trend line through the larger values that were believed to represent the true population sizes. This was achieved by using quantile regression (RQ) (Koenker 2009), which provides, in certain circumstances, a more appropriate picture of the relationships between variables that are obscured by other regression methods such as least squares regression (LR) (Cade and Noon 2003). Specifically, the regression of the 95th quantile was computed, so that less emphasis was placed on anomalously small counts in the time series. This was applied within a weighted regression model, whereby a 95th quantile function was fitted to each count in the time series of each colony, with the weights decreasing exponentially with the number of years on either side of the "target" year. For each colony, each year of the time series between the first and the last census was made the target year, in turn (irrespective of whether a census occurred in that year or not). The weighting function was

$$w_j = \exp\left(-\left(\frac{(t-j)}{\sigma}\right)^2\right) \tag{1}$$

where j is year 1, 2,. . .i, commencing from the first census year for each colony, t is the target year and σ is the smoothing constant (Underhill *et al.* 2006). The smoothing constant was set at 3.5 for most colonies. The chosen value of σ was based on the fact that for most colonies, the widest gap between census years was five years. With σ set at 3.5, the years on each side of the target year t (which has a weight of 1) have a weight of 0.92, and the weight decreases exponentially in both directions so that the fifth year on either side of the target year has a weight of 0.12. The weights attached to years more than five from the target year were 0.05 and smaller, and were therefore inconsequential in the analysis. A smaller weighting function giving consequence for example only as far as 4 yr on either side of the target year could have resulted in unreliable predictions where a gap of 5 yr occurred in the time series. The value of 3.5 was therefore selected as a compromise between avoiding nonsensical predictions caused by data gaps, and "over-smoothing" the data with fitted trends using larger values of σ. However, at a few colonies, in particular, some of the new colonies, gaps of up to 10 yr without data occurred. For these colonies it was necessary to set the smoothing constant at 7.0 to prevent nonsensical predictions. These colonies were (in order of their distance the eastern-most extent of the range) Geyser Rock, Cape Columbine, Buchu Twins, Marshall Reef, Klein Ichaboe, Dolphin Head, Sylvia Hill, Pelican Point, and Torra Bay.

The 95th quantile regression coefficients were used to predict pup numbers in each year t and to provide a "moving rate of change" (Underhill *et al.* 2006) between the first and final counts for each colony. The essential difference between the RQ model and an LR model (using the same weighting functions) is that whereas the former constructs a trend line that represents the upper 95th quantile and so passes among the larger values in the time series (placing reduced emphasis on small values), the latter generates a trend line that passes through the middle of the values in the

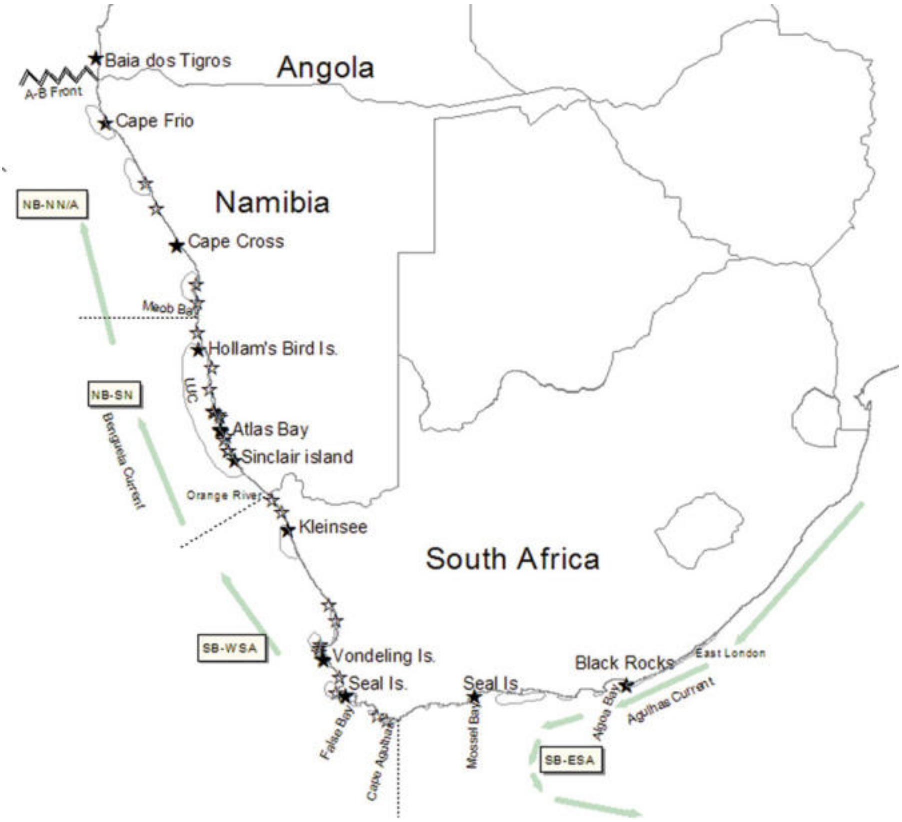

Figure 1. Map showing selected Cape fur seal breeding colonies in South Africa, Namibia and Angola, and locations mentioned in the text. The abbreviations in the boxed labels represent the following: NB-NN/A = Northern BCLME–North Namibia/Angola, NB-SN = Northern BCLME–South Namibia, SB-WSA = Southern BCLME–West South Africa, SB-ESA = Southern BCLME–East South Africa.

time series (placing equal emphasis on all values). For comparison with the outcomes of the RQ models, LR models were also applied to the pup data, using the same weighting functions, although the RQ-predicted pup values were expected to be the better indicators of numerical trends for the population (all age classes) for the reasons given above. Therefore RQ models were used to classify the breeding status of colonies (see previous subsection).

The analyses were performed in R (R 2.9.0, R Development Core Team), incorporating the "quantreg" package (Koenker 2009). Results were reported per colony for the entire time series, and to aid with distinguishing general patterns in space and time, were also summarized into before and after 1990. To assist with interpretation of numerical patterns in terms of geography, colonies were grouped as being island or mainland colonies, or were grouped into two main geographical areas, each of which were further divided into two areas. The two main areas were divided at the Orange River (Fig. 1) which has been used as proxy for the boundary between the Southern Benguela Current Large Marine Ecosystem (BCLME) and Northern BCLME (van der

Lingen *et al.* 2006), of which the former extends around the coast of South Africa to East London (Watermeyer *et al.* 2008) (Fig. 1); thus it was appropriate to refer to the two areas as the Southern BCLME and the Northern BCLME. The former was further divided into the east (East SA) and west (West SA) coasts of South Africa, separated at Cape Agulhas (Fig. 1); the latter was divided into the Namibian coast from Meob Bay southwards (South Namibia), which approximately coincides with the position of the Lüderitz upwelling cell between 25°S and 28°S (Peard 2007), and the area to the north of Meob Bay including northern Namibia and southern Angola (North Namibia–Angola) (Fig. 1).

Changes in Spatial Distribution

The change in distribution of the seal breeding population since the 1970s was determined from the number of pups estimated per colony using weighted regression models (see above), the number of breeding colonies in existence (determined by predictions of the weighted quantile regression models performed on the pup count time series of the colonies), and the "along the path" distance around the coastline from the eastern boundary of Algoa Bay (33°46.03′S, 26°19.45′E), close to the eastern-most colony at Black Rocks (Fig. 1). The "center of distribution" (CoD) of the breeding population in each year was estimated as

$$\mathrm{CoD} = \frac{\sum d^{*}n}{\sum n} \tag{2}$$

where d is the shortest distance around the coast of each colony from the fixed point, calculated using the "along the path distances" option of the Pathmatrix extension in Arcview GIS 3.3 (Environmental Systems Research Institute, Inc.); and n is the predicted number of pups per colony per year. Because the weighted regression analysis effectively considered counts up to five years on either side of the target year in most cases (see above), the CoD was calculated for each sixth year of the time series, starting in 1976 (the first comprehensive census year in this study). This was to avoid autocorrelation of residuals as CoD estimates were themselves subjected to regression analysis to determine whether significant directional shifts occurred over the time series. Only colonies classified as breeding colonies were considered in the analysis (*e.g.,* a new colony such as Cape Frio was considered only from when the predicted pup number from regression analysis exceeded 100).

RESULTS

Temporal Changes in Pup Numbers

For most of the colonies the patterns in the rates of change (the slopes of the regression models) were similar between the RQ and the LR regression approaches, although RQ models were less sensitive to variability in pup numbers and their annual predictions of pup numbers were generally larger than the LR model predictions (Fig. 2, 3), as expected. The average rates of change obtained by using each of the two weighted regression models (RQ and LR) were highly correlated for each of these two periods (Pearson's r: 1972–1990 = 0.88, 1991–2009 = 1.00), therefore only the results of the RQ models are presented in Table 1. Of the 45 colonies recognized

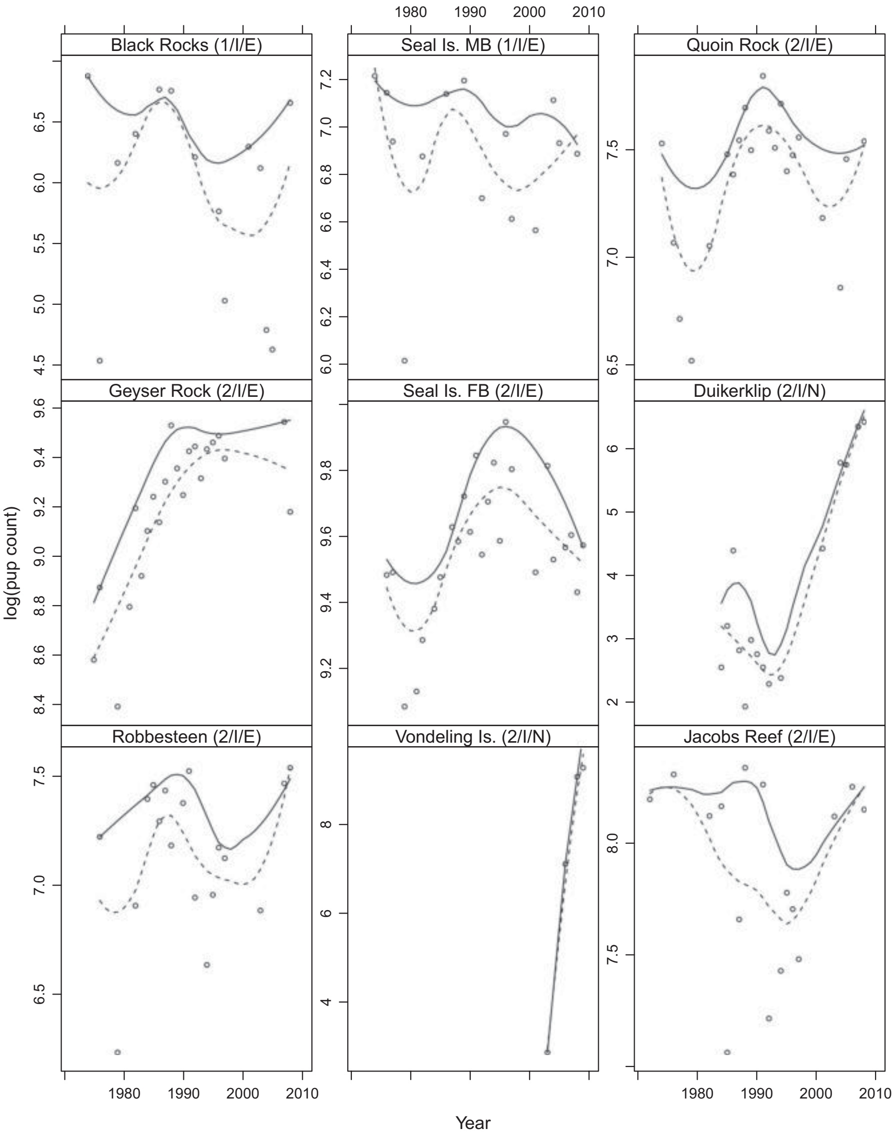

Figure 2. Smoothed predicted curves fitted to log transformed (natural logarithms) raw counts of Cape fur seal pups at breeding colonies in the southern BCLME, estimated using weighted 95th quantile (solid line) and least squares (dashed line) regression models. In the parentheses, the numbers 1 or 2 indicate the areas East South Africa (1) or West South Africa (2), respectively; I or M indicate island or mainland breeding colony, respectively; and E or N indicate established or new breeding colony, respectively.

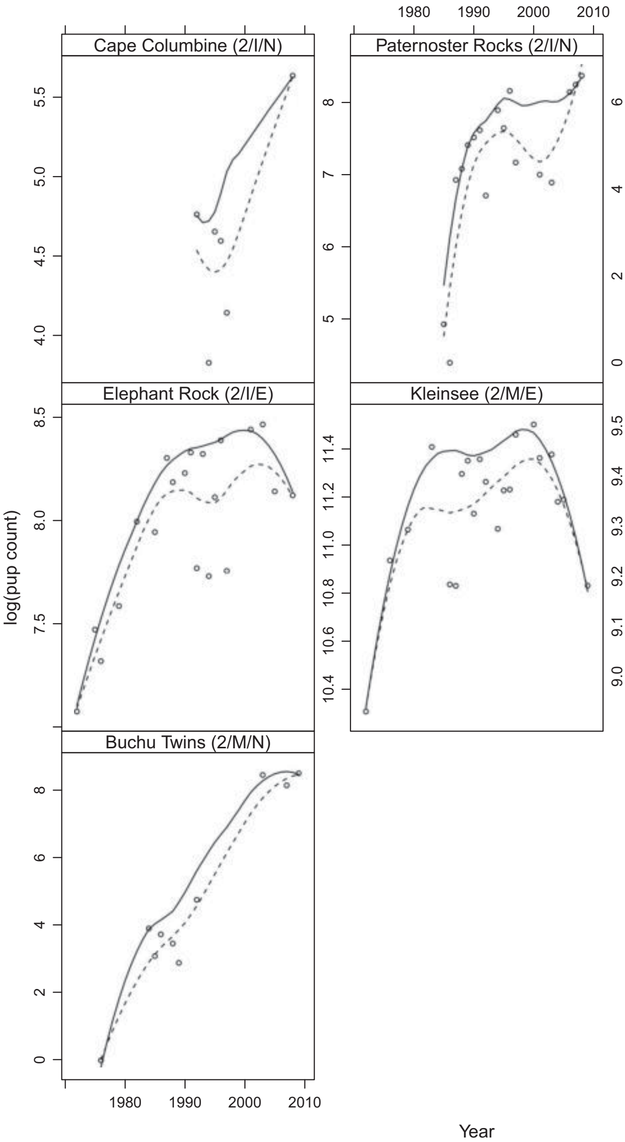

Figure 2. (Continued)

in Table 1, 40 (24 island and 16 mainland) were classified as breeding colonies at the end of the time series, based on the application of the RQ model to the times series of pup counts per colony, and the definition of Oosthuizen and David (1988). According to this, there are currently 17 more breeding colonies than at the start of the time series, a 74% increase. Of the remaining five colonies in Table 1 at which pups have been recorded during the time series, Mercury Island remained extinct after seals were displaced from there during a management intervention in the late

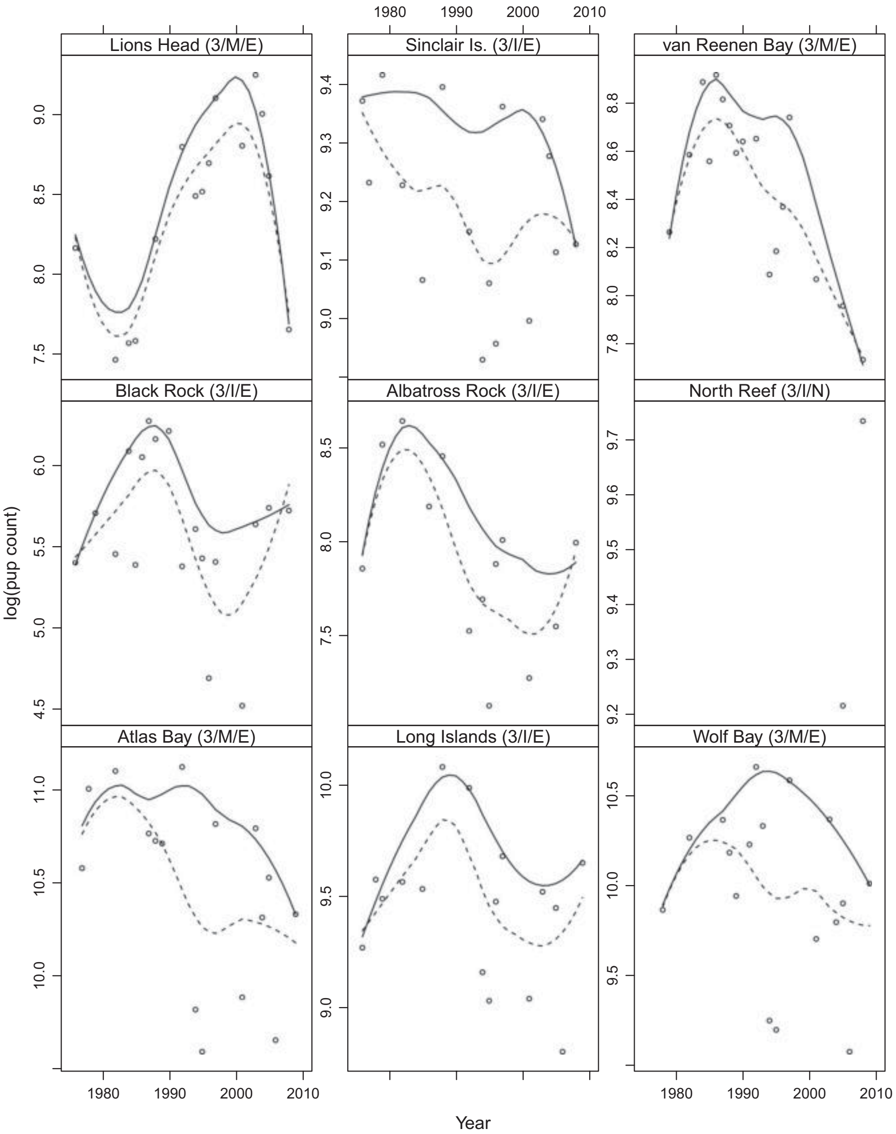

Figure 3. Smoothed predicted curves fitted to log transformed (natural logarithms) raw counts of Cape fur seal pups at breeding colonies in the Northern BCLME, estimated using weighted 95th quantile (solid line) and least squares (dashed line) regression models. In the parentheses, the numbers 3 or 4 indicate the areas South Namibia (3), or North Namibia/Angola (4), respectively; I or M indicate island or mainland breeding colony, respectively; and E or N indicate established or new breeding colony, respectively.

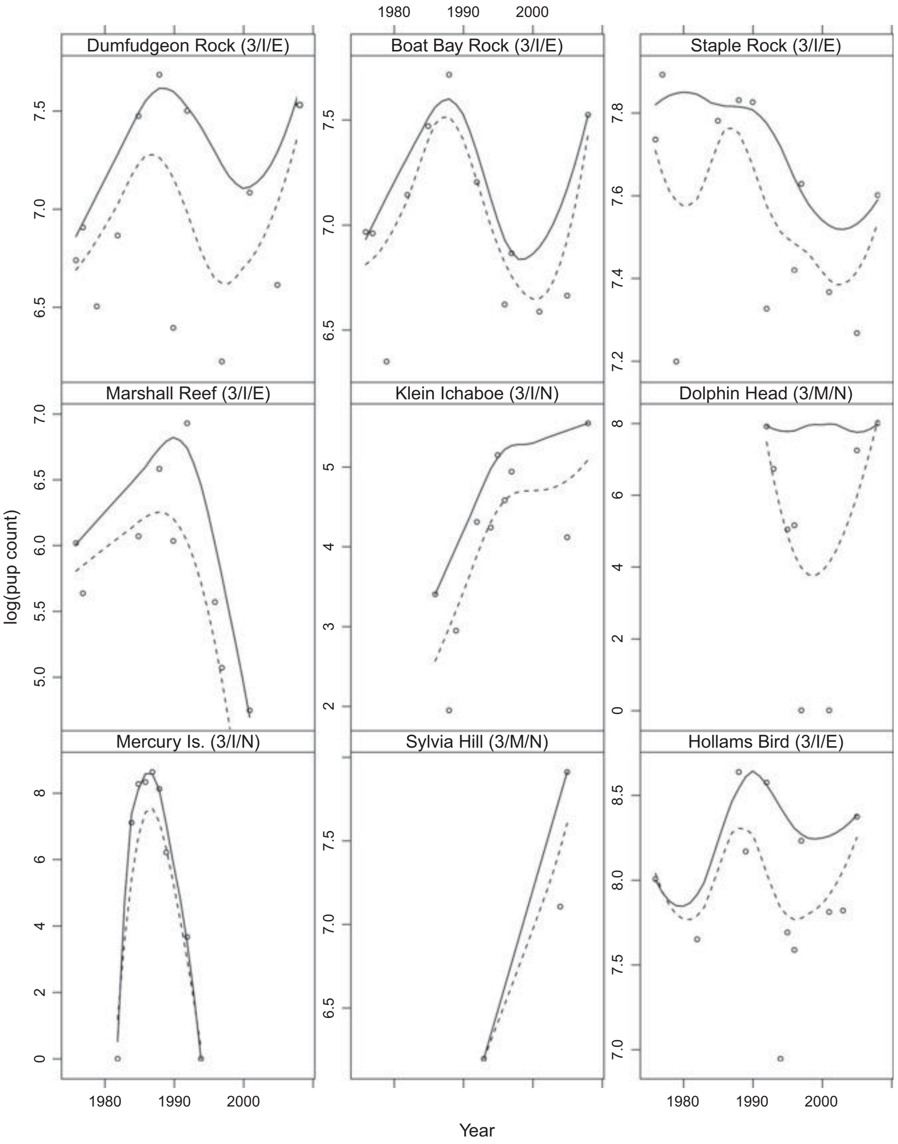

Figure 3. (Continued)

1980s and four others did not fulfill the accepted definition of a breeding colony at the end of the time series.

In the period 1972–1990, 90% of colonies exhibited net positive growth; slight net declines (<0.02% per annum) occurred at just three sites (Table 1). Post-1990, 25% of established colonies and 80% of new ones displayed net positive growth (Table 1). Growth was most evident in West South Africa and in North Namibia–Angola, where new colonies outnumbered established colonies during the latter

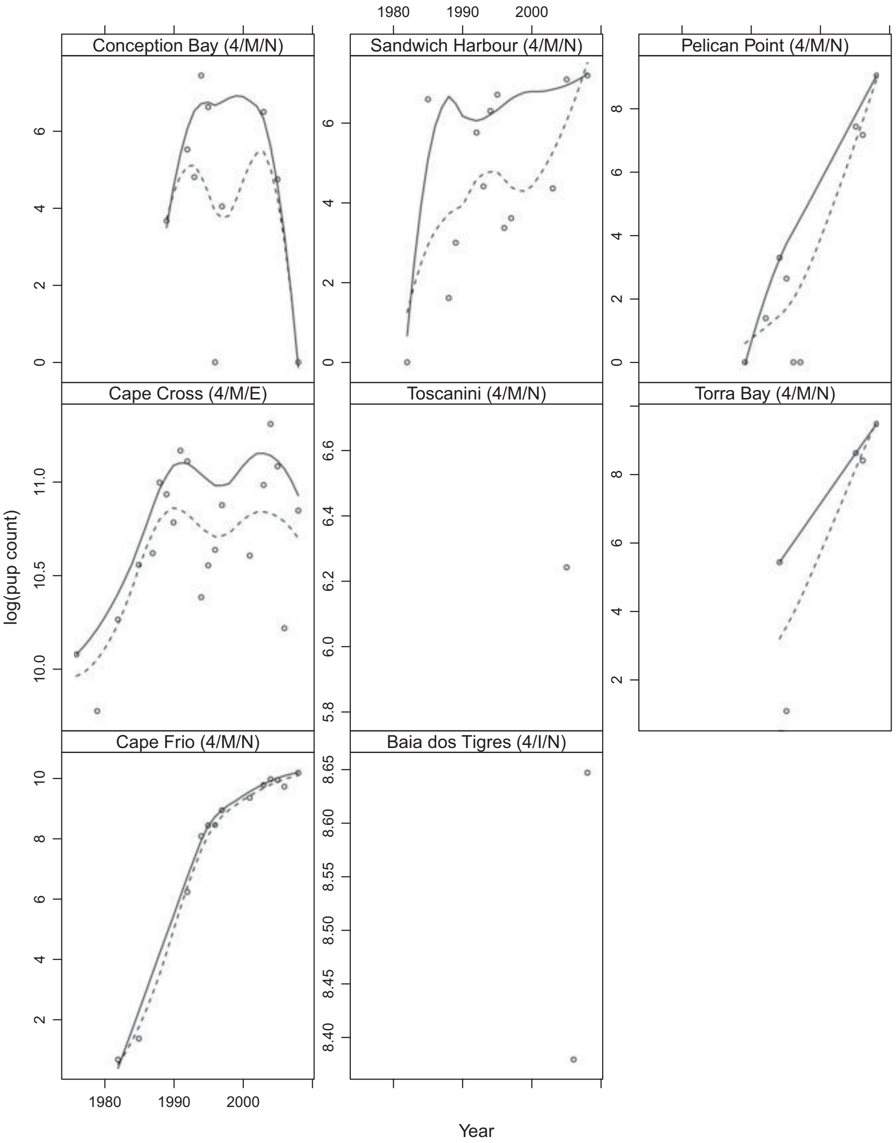

Figure 3. (Continued)

period (Fig. 2, 3). Most of the established Namibian colonies, which except for Cape Cross occur in South Namibia, fluctuated or declined during the second half of the time series (Fig. 3).

When summing the predicted values of pup numbers at all colonies per year, the results of both model types indicated that there was little or no growth since the early 1990s in either the Northern BCLME or the entire region (Fig. 4). However, growth in the Southern BCLME was positive until the early 2000s, before numbers declined. This largely reflected the trend at the largest colony, Kleinsee (Fig. 2) which accounted for *ca.* two-thirds of pup numbers in South Africa in 2000, dropping to *ca.* 50% of its predicted zenith in 2006 and further to *ca.* 44% by 2009, according to both models. With regard to the Northern BCLME, there was a considerable shift of 17% (according to both model types) in the ratio of numbers from South Namibia to North Namibia–Angola from 1990 to 2009 (Fig. 4).

Changes in Spatial Distribution

Shifts in the CoD and range of the seal breeding population during the study period are shown in Figure 5. Whereas the eastward range of the breeding population remained constant throughout the time series, the northward range was extended by *ca.* 680 km (from Cape Cross to Baia dos Tigres in Angola) during the latter part of the time series (Fig. 5.1). There was a significant shift in the CoD of the breeding population over the entire range, at a rate of 5.82 km/yr over the thirty year period (SE = 0.90; $F_{1,4} = 41.70, P = 0.003, r^2 = 0.92$), northward (or clockwise in relation to the coastline). The northward range extension of the breeding population in the Northern BCLME (Fig. 5.2) is implicit in the northward extension of the entire population, but the range of the breeding population in Southern BCLME was also extended northward during the time series (Fig. 5.3), by *ca.* 105 km (from Kleinsee to Buchu Twins). However, whereas the shift in CoD of the northern colonies was significant (7.20 km/yr, SE = 1.39, $F_{1,4} = 26.66, P = 0.006, r^2 = 0.87$), the latter was not (0.30 km/yr, SE = 0.67; $F_{1,4} = 0.23, P = 0.66, r^2 = 0.05$). The distances of new breeding colonies from breeding colonies that were already existing (including established colonies or new colonies that were already in existence at the time) was greatest in North Namibia–Angola (Fig. 6).

DISCUSSION

As is the case with fur seal populations elsewhere in the world that have recovered from past over-exploitation (*e.g.,* Boyd 1993, Arnould *et al.* 2003, Hofmeyr *et al.* 2006, Kirkwood *et al.* 2009) there is interest with regard to the dynamics of the Cape fur seal population including trends, its relationship to the precommercial sealing population and to the carrying capacity of the environment (*e.g.,* Butterworth *et al.* 1988, Kirkman 2009). This study used spatio-temporal trends in pup counts as indicators of the changes in size and distribution of the Cape fur seal population, as has been done in several studies of seal populations elsewhere (*e.g.,* Hofmeyr *et al.* 2005, Kirkwood *et al.* 2005, Hofmeyr *et al.* 2006). Previously, Kirkman *et al.* (2007) concluded from trends in pup counts that growth of the Cape fur seal population up to 1993 (reported by Butterworth *et al.* 1995) stabilized subsequently, and that the population in 2003 was similar in size to 10 yr previously. However, that study considered mainly established breeding colonies and did not take into account several locations previously classified by Oosthuizen and David (1988) as nonbreeding colonies, such as Buchu Twins, Conception Bay and Pelican Point, the establishment of other new colonies such as Cliff Point and Baia dos Tigres, or increases in pup production at many of these locations. This was because several of these locations were censused infrequently or not at all up until 2003. This was rectified in the present study, which considers a 6 yr longer time series compared to Kirkman *et al.* (2007), by including all colonies at which births have been recorded during aerial

Table 1. The locations of all Cape fur seal breeding colonies in South Africa, Namibia and Angola for which pup counts of >0 have been obtained during one or more aerial censuses since 1972, in clockwise order with regard to the coastline, starting at the southeastern-most colony. The mean annual rate of change (with standard error) for the periods 1972–1990 and 1991–2009 was estimated using weighted 95% quantile regression models only for colonies where more than 100 pups have been counted during at least one census. Colonies with the superscript 1 were established breeding colonies in 1972; colonies that did not fit the definition of a breeding colony in 2009 based on the prediction of the weighted quantile regression equation or due to their being insufficient data to fit the model, have superscript 2; I or M under "Type" refers to "island" or "mainland" colonies respectively; Under "Area," NB and SB refer to Northern and Southern BCLME, respectively, ESA and WSA refer to East and West South Africa, respectively, SN and NN/A refer to South Namibia and North Namibia/Angola, respectively.

Name of breeding colony	Latitude (south)	Longitude (east)	Type	Area	Mean rate of change ± SE for 1972–1990; the number of censuses are in ()	Mean rate of change ± SE for 1991–2009; the number of censuses are in ()
1. Black Rocks^1	33°50.27′	26°15.80′	I	SB-ESA	−0.0212 ± 0.0205(6)	0.0100 ± 0.0804(8)
2. Robberg^2	34°06.00′	23°23.13′	M	SB-ESA	– (0)	– (3)
3. Seal Is. (Mossel Bay)^1	34°09.02′	22°07.02′	I	SB-ESA	−0.0087 ± 0.0080(7)	−0.0194 ± 0.0320(7)
4. Quoin Rock^1	34°47.23′	19°40.10′	I	SB-WSA	0.0034 ± 0.0219(10)	−0.0169 ± 0.0324(11)
5. Geyser Rock^1	34°41.32′	19°24.75′	I	SB-WSA	0.0431 ± 0.0060(13)	0.0016 ± 0.0050(9)
6. Seal Is. (False Bay)^1	34°08.30′	18°35.00′	I	SB-WSA	0.0306 ± 0.0090(11)	−0.0148 ± 0.0318(14)
7. Duikerklip	34°03.50′	18°18.13′	I	SB-WSA	0.1405 ± 0.1108(7)	0.1601 ± 0.1907(8)
8. Robbesteen^1	33°38.63′	18°24.10′	I	SB-WSA	0.0192 ± 0.0068(9)	0.0127 ± 0.0763(9)
9. Vondeling Is.	33°09.07′	17°58.82′	I	SB-WSA	– (0)	1.1983 ± 0.2368(4)
10. Jutten Is.^{2}	33°04.80′	17°57.17′	I	SB-WSA	– (0)	– (3)
11. Jacob's Reef^1	32°57.30′	17°51.70′	I	SB-WSA	0.0103 ± 0.0060(7)	−0.0186 ± 0.0737(9)
12. Cape Columbine	32°49.55′	17°50.70′	I	SB-WSA	– (0)	0.0356 ± 0.0415(6)
13. Paternoster Rocks	32°44.30′	17°52.30′	I	SB-WSA	0.3228 ± 0.0796(6)	0.0613 ± 0.1038(11)
14. Bird Is.	32°05.28′	18°18.13′	I	SB-WSA	0.0659 ± 0.0368(7)	0.1853 ± 0.2571(11)
15. Elephant Rock^1	31°38.63′	18°08.65′	I	SB-WSA	0.0659 ± 0.0090(9)	−0.0155 ± 0.0386(11)
16. Kleinsee^1	29°34.17′	16°59.80′	M	SB-WSA	0.0557 ± 0.0145(9)	−0.0052 ± 0.0263(12)
17. Cliff Point	29°05.90′	16°49.10′	M	SB-WSA	– (0)	−0.1526 ± 5.4728(4)
18. Buchu Twins	28°45.57′	16°33.78′	M	SB-WSA	0.2338 ± 0.0452(6)	0.1412 ± 0.1674(4)

(Coontinued)

Table 1. (Continued)

Name of breeding colony	Latitude (south)	Longitude (east)	Type	Area	Mean rate of change ± SE for 1972–1990; the number of censuses are in ()	Mean rate of change ± SE for 1991–2009; the number of censuses are in ()
19. Lion's Head[1]	27°40.33′	15°31.40′	M	NB-SN	0.0403 ± 0.0266(5)	−0.0716 ± 0.1734(10)
20. Sinclair Is.[1]	27°40.00′	15°31.30′	I	NB-SN	−0.0072 ± 0.0078(6)	−0.0098 ± 0.0322(10)
21. van Reenen Bay[1]	27°24.00′	15°21.00′	M	NB-SN	0.0268 ± 0.0220(9)	−0.0462 ± 0.0470(8)
22. Black Rock[1]	27°23.40′	15°21.00′	I	NB-SN	0.0581 ± 0.0111(9)	−0.0235 ± 0.0655(9)
23. Albatross Rock[1]	27°07.00′	15°14.30′	I	NB-SN	0.0331 ± 0.0269(5)	0.0300 ± 0.0746(8)
24. North Reef	27°00.00′	15°11.40′	I	NB-SN	– (0)	0.1728 ± 2.0599(2)
25. Atlas Bay[1]	26°49.92′	15°07.90′	M	NB-SN	0.0385 ± 0.0324(6)	−0.0301 ± 0.0339(11)
26. Long Is.[1]	26°49.33′	15°07.20′	I	NB-SN	0.0455 ± 0.0146(6)	−0.0251 ± 0.0348(11)
27. Wolf Bay[1]	26°48.67′	15°07.20′	M	NB-SN	0.0566 ± 0.0093(5)	−0.0191 ± 0.0212(13)
28. Dumfudgeon Rock[1]	26°29.67′	15°07.20′	I	NB-SN	0.0367 ± 0.0130(7)	0.0173 ± 0.0738(5)
29. Boat Bay Rock[1]	26°25.33′	15°05.50′	I	NB-SN	0.0385 ± 0.0165(6)	0.0035 ± 0.0945(6)
30. Staple Rock[1]	26°21.33′	14°59.00′	I	NB-SN	0.0089 ± 0.0109(6)	−0.0119 ± 0.0313(6)
31. Marshall Reef[1,2]	26°21.60′	14°57.60′	I	NB-SN	0.0569 ± 0.0023(5)	−0.2612 ± 0.0943(6)
32. Klein Ichaboe	26°17.40′	14°55.80′	I	NB-SN	0.1933 ± 3.0707(3)	0.0849 ± 0.0788(7)
33. Dolphin Head	25°44.00′	14°49.92′	M	NB-SN	– (0)	−0.0085 ± 0.1950(8)
34 Mercury Island[2]	25°43.17′	14°50.10′	I	NB-SN	1.2476 ± 1.2086(7)	– (2)
35. Sylvia Hill	25°08.03′	14°51.15′	M	NB-SN	– (0)	0.1427 ± 1.2342(3)
36. Hollam's Bird Is.[1]	24°38.33′	14°31.80′	I	NB-SN	0.0195 ± 0.0245(4)	−0.0119 ± 0.0654(8)
37. Conception Bay	23°55.80′	14°29.40′	M	NB-NN/A	0.7553 ± 2.8311(1)	−0.4554 ± 0.7619(9)
38. Sandwich Harbour	23°21.00′	14°28.80′	M	NB-NN/A	0.6865 ± 0.2671(4)	0.1213 ± 0.2122(9)
39. Pelican Point	22°52.50′	14°26.60′	M	NB-NN/A	0.6591 ± 2.6645(1)	0.4417 ± 0.0806(8)
40. Cape Cross[1]	21°46.50′	13°57.00′	M	NB-NN/A	0.0731 ± 0.0095(8)	−0.0244 ± 0.0732(12)
41. Toscanini	19°23.82′	13°22.80′	M	NB-NN/A	– (0)	– (1)
42. Torra Bay	19°27.60′	13°15.00′	M	NB-NN/A	– (0)	0.2882 ± 0.0026(5)
43. Möwe Bay[2]	19°22.67′	12°42.27′	M	NB-NN/A	– (0)	–
44. Cape Frio	18°26.17′	12°00.20′	M	NB-NN/A	0.4889 ± 0.0474(2)	0.2281 ± 0.0977(11)
45. Baia dos Tigres	16°38.40′	11°43.20′	I	NB-NN/A	– (0)	0.1337 ± 3.7829(2)

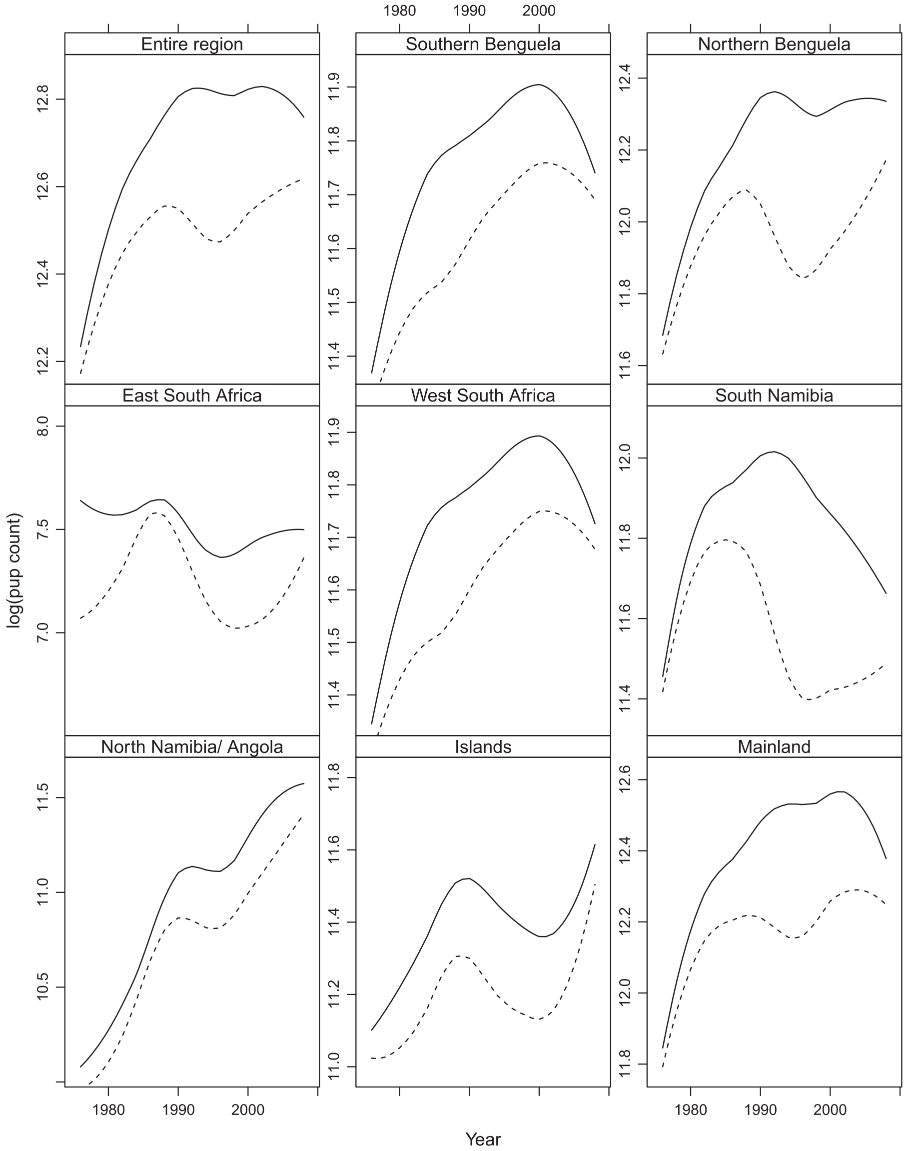

Figure 4. Summed predicted pup counts per year for all Cape fur seal breeding colonies of the entire region and for the different areas and types of colonies presented in Table 1, showing differences between the predictions of weighted 95th quantile (upper ends of vertical lines) and least squares (lower ends of vertical lines) regression models.

photographic censuses conducted since 1972. By summing the annual number of pups predicted by the regression models of all the individual breeding colonies in this study (Fig. 4), it was possible to look at trends in predicted pup numbers for the population. Although the predicted values and the consequent trends differed between the two model types (RQ and LR), both supported the finding of Kirkman

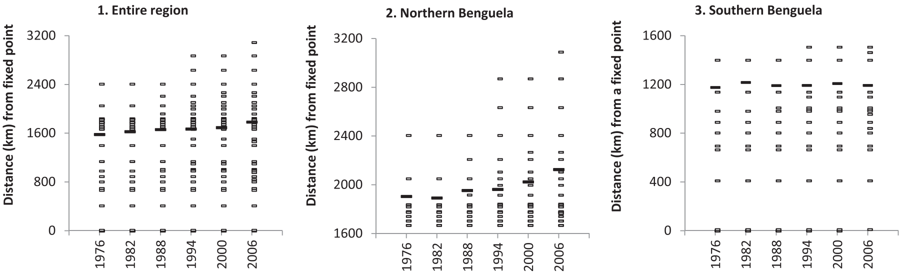

Figure 5. The location of all Cape fur seal breeding colonies (small gray bars) present in the entire region, the Northern Benguela and the Southern BCLME, at different times in the study period, in terms of their distance along the coast from the eastern boundary of Algoa Bay, South Africa. The long black markers represent the "center of distribution" of the breeding population per year, based on the application of equation 2 to the time series of predicted counts per colony (determined using weighted 95th quantile regression analysis). Note the differences in scale of the y-axes between the panels.

et al. (2007) that there has been little overall growth in the population since the early 1990s.

Roux (1987) proposed a conceptual model in which he classified the process of recolonization of the Amsterdam Islands by the subantarctic fur seal *Arctophoca tropicalis*, following depletive human exploitation, into four phases: (1) a "survival" phase extending from the cessation of exploitation to the initiation of breeding, where surviving individuals ensured that a remnant population persisted at isolated and remote sites; (2) an "establishment" phase during which breeding was restricted to a few founding colonies; (3) a "recolonization" phase during which numbers increased and new colonies arose in response to a shortage of space in the founding colonies; and (4) a "maturity" phase in which the rate of increase declined, caused by density-dependent factors such as an absolute shortage of space ashore or food at sea. This model has been shown to be applicable to the patterns of expansion of other otariid populations recovering from overexploitation, including subantarctic fur seals at Marion Island (Hofmeyr *et al.* 2006), New Zealand fur seals *Arctophoca australis forsteri* on the Otago Peninsula (Bradshaw *et al.* 2000) and South American sea lions *Otaria byronia* in Patagonia (Grandi *et al.* 2008). Although these descriptions involved populations situated on oceanic islands or on mainland peninsulas, which were localized relative to the extensive range of Cape fur seals, the model seems to be broadly applicable to the expansion of the Cape fur seal population since the early 20th century (when sealing was placed under legal controls, Shaughnessy 1984). Persistence of "remnant" colonies on small island locations was comparable with the first two phases of Roux's (1987) paradigm, "survival" and "establishment." The return of seals to some of the colonies at which they had been extirpated, including Sinclair Island (by the late 19th century), Seal Island in False Bay and Albatross Rocks (both before the 1950s) (Shaughnessy 1984) may have marked the beginning of the "recolonization" phase. At the time however, seals were prevented from reoccupying most of the other locations of extinct colonies due to human occupation and in many cases, management of the islands for the production of seabird products (guano, eggs) with deliberate exclusion of seals (Rand 1952, Shaughnessy 1984); breeding colonies subsequently developed on the mainland, including at Kleinsee, Atlas Bay,

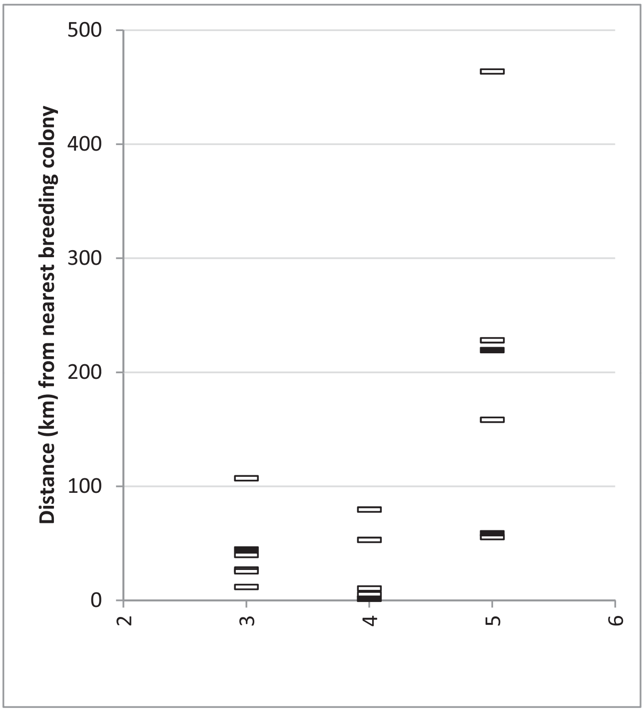

Figure 6. The distance (km) of each new breeding colony, distinguished according to the geographical area that they occur in, from the nearest breeding colony in existence at the time it was first classified as a breeding colony. Plain markers indicate that the nearest breeding colony was an old one, and solid markers that it was a new one. WSA = West South Africa, SN = South Namibia, NN/A = North Namibia.

and Wolf Bay, purportedly around the middle of the 20th century. These colonies and the one at Cape Cross were responsible for most of the population growth between then and the early 1990s (Wickens *et al.* 1991, Butterworth *et al.* 1995). In effect therefore, "colonization" may be an appropriate term for this phase of the Cape fur seal's population expansion (as opposed to "recolonization").

On the face of it, the lack of overall growth in the population since the early 1990s based on predicted pup numbers (Fig. 4) appears suggestive of the population having attained an equilibrium state, as in the "maturity" phase of Roux's model. Instead, the establishment and growth of several new breeding colonies, the substantial fluctuations and/or declines in pup numbers that were evident at several other colonies, and the northwards shift in the population's range, appear to indicate a highly dynamic state. Potential causes of the observed patterns are discussed below.

Potential Causes of Spatio-temporal Changes During the Study Period

Space limitation—In the study period, there was a proliferation of 17 new breeding colonies in less than 30 yr (a 74% increase). Most of the sites where new breeding colonies now occur are known to have been nonbreeding colonies previously

(Shaughnessy 1987, Oosthuizen and David 1988, DEA[3]). The formation of non-breeding colonies and their transition to breeding colonies is characteristic of the "recolonization" phase in other otariid populations, and generally has been attributed to saturation of space at source breeding colonies (*e.g.,* Bradshaw *et al.* 2000, Grandi *et al.* 2008). Space limitation is a potential mechanism of density dependence at least for the island colonies: all the island breeding colonies that were in existence at the beginning of the study period are on small islands (3 ha in area or less) and are typically crowded during the breeding season (Rand 1967; SPK, personal observation). Indeed, the patterns of decelerating growth with time which were evident at certain island colonies (*e.g.,* Geyser Rock, Paternoster Rocks, and Elephant Rock, see Fig. 2) may be consistent with breeding space limitation.

However, whereas new colonies that develop as a result of space limitation would be expected to form nearby to the source colony if there is habitat available (*e.g.,* Bradshaw *et al.* 2000, Grandi *et al.* 2008), many of the new breeding colonies were formed in remote areas of West South Africa and the areas further north, relatively distant from the nearest potential source colonies. For example, nine new breeding colonies were in excess of 50 km from the nearest potential source colony (Fig. 6). This is notwithstanding that there does not appear to be any shortage of space on the mainland in the vicinity of established breeding colonies in much of the Northern BCLME or the northern part of the Southern BCLME, where the greater part of the coastline is restricted or protected area with relatively little human interference (Kirkman *et al.* (2007). For these reasons it seems unlikely that space limitation on its own was accountable for the formation and growth of new breeding colonies, although it may have been relevant to certain island colonies or may have acted in combination with other factors (see below).

Food limitation—Another possible mechanism of density dependence is food limitation, whereby prey availability within the foraging range of the breeding population of a colony is diminished with increasing population density. This may explain the patterns of decelerating growth with time at certain mainland breeding colonies (*e.g.*, Kleinsee, Buchu Twins, Sandwich Harbour, and Cape Frio; see Fig. 2, 3), at which breeding space does not appear to be limiting (Wickens *et al.* 1991; SPK, personal observation). However, whereas density dependence has been implicated in changing population growth rates or with influencing factors that affect population growth rates (*e.g.*, Doidge *et al.* 1984, Fowler 1990, Etnier 2004, Drago *et al.* 2011), it was generally difficult to positively recognize density dependence among the wide variety of growth patterns at breeding colonies in this study (Fig. 2, 3). Effects of environmental events or other stresses that prevent colonies from reaching saturation in terms of resources (breeding space or prey) may contribute to this. The importance of environmental variability as a density independent influence on the population dynamics of seals has been emphasized by several authors (*e.g.,* Trillmich 1993, Gerber and Hilborn 2001, Forcada *et al.* 2005, Reid and Forcada 2005, Becker *et al.* 2009) and according to Krebs (2002) its confounding effects may be the reason that density dependence has rarely been positively identified at the scale of wildlife populations.

In the Northern BCLME, overfishing (Boyer and Hampton 2001) and severe environmental perturbations that occurred between 1993 and 1995 (Gammelsrød *et al.* 1998) were responsible for severe depletion of fish stocks, including prey of seals such

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[3] Department of Environmental Affairs Branch Oceans and Coasts, Private Bag x2, Roggebaai 8012, Cape Town. January 2010.

as sardine *Sardinops sagax*, anchovy *Engraulis encrasicolus*, and hake *Merluccius* spp. (van der Lingen *et al.* 2006). Reduced survival rates (especially of pups) and pregnancy rates of Cape fur seals were attributed to the resulting unfavorable feeding conditions (Roux 1998), and led to relatively low pup counts at most Northern BCLME breeding colonies in the mid-1990s (Fig. 3). Prey resources for top predators remained in a depleted state in South Namibia for at least the next decade (Cury and Shannon 2004, van der Lingen *et al.* 2006). It is likely that this was also influenced by the below average upwelling volumes that characterized the Lüderitz upwelling cell (Peard 2007), which coincides approximately with South Namibia (Fig. 1) and is the most powerful driver of ocean productivity in the Northern BCLME (Bakun 1996), in this period.

Further consequences of the above were that the distributions of certain prey stocks shifted northward (Boyer and Hampton 2001, van der Lingen *et al.* 2006). In particular, the availability of horse mackerel *Trachurus trachurus capensis* for top predators as well as fisheries in North Namibia–Angola increased (Axelsen *et al.* 2004, Mecenero *et al.* 2007). These shifts in prey availability correspond with the directionality of the shift in the Cape fur seal breeding population in the Northern BCLME, which was mainly attributable to the development of new breeding colonies in North Namibia–Angola (Fig. 5). In the latter area, *ca.* 90% of the current breeding colonies are new colonies (see Table 1), at least three of which increased at rates greater than 20% per annum during the latter half of the study (Pelican Point, Torra Bay and Cape Frio) (Table 1). The maximum intrinsic annual rate of increase of seal populations is *ca.* 17% (Payne 1977) and is likely to be lower at mainland Cape fur seal colonies, considering predation of pups by terrestrial predators including brown hyena, *Hyaena brunnea*, and black-backed jackal, *Canis mesomelas* (Oosthuizen *et al.* 1997, Wiesel 2006). Therefore these rates of increase must have been sustained by immigration of animals from other breeding colonies.

Immigrants to North Namibia–Angola may have stemmed from as far south as South Africa: Oosthuizen (1991) previously documented that dispersal from the South African colonies to Namibian colonies especially Cape Cross was not uncommon, based on tag retrievals. However, based on the pup count trends, the most obvious source of immigrants to North Namibia–Angola colonies is from South Namibia, where numbers per colony declined more or less proportionally to the increase in the former area (Fig. 4). South Namibia contains nearly all of the established Namibian colonies (with the exception of Cape Cross in North Namibia–Angola), most of which were characterized by variable recruitment during the second half of the time series (1991–2009, Fig. 3) with associated negative rates of change during that period (Table 1).

The supposition that feeding conditions were generally more favorable in North Namibia–Angola than in South Namibia was supported by the findings of a comparative satellite telemetry investigation in 2002–2004 (Skern-Mauritzen *et al.* 2009). Study animals including lactating females tagged at Cape Frio in the north displayed fidelity both to their colony and to foraging areas, suggesting reliable prey resources nearby. In contrast, study animals from Atlas Bay in the south displayed foraging behavior that was indicative of poor feeding conditions, including long foraging trips, low fidelity to their tagging colony and to foraging areas, and displacement to other colonies. The colonies that they relocated to were almost invariably to the north and included Conception Bay, Sandwich Harbour, Pelican Point, Cape Cross, Torra Bay, Cape Frio, and Baia dos Tigres (all sites of new breeding colonies with the exception of Cape Cross).

The numbers of breeding colonies in the Southern BCLME were quite stable during the study period relative to the Northern BCLME (Fig. 4). This may be explained by the general stability of South Africa's marine environment (including prey resources) during the study period (Cury and Shannon 2004, van der Lingen *et al.* 2006). However, it may also be attributable to other factors. These include there being less likelihood of human disturbance at existing breeding colonies that could cause seals to disperse to other locations (*i.e.,* sealing activities discussed below), or a lack of suitable alternative breeding habitat, particularly in East South Africa and the southern part of West South Africa, due to greater human presence than in the remote, restricted areas or reserves that characterize much of the coastline of the northern part of West South Africa and the Northern BCLME.

Human disturbance—Human disturbance was proposed by Rand (1972) as a causal factor in the development of new seal breeding colonies during the 20th century. Examples are the establishment of Atlas Bay and Wolf Bay colonies due to displacement from nearby Long Islands (Rand 1972). Other cases that have been cited include the establishment of a colony on Mercury Island and a large influx of seals to the colony at Cape Cross in the 1980s following large-scale disturbance of the colonies at Atlas Bay and Wolf Bay (Crawford *et al.* 1989, Wickens *et al.* 1991), and the development of the colony at Dolphin Head on the Namibian mainland when seals were deliberately displaced from nearby Mercury Island in the interests of seabird conservation (Crawford *et al.* 1994, Kirkman 2009). Except in the latter case, it was known that human disturbance at the purported source colonies was in the form of sealing during the breeding season (*i.e.,* November–December), the time of year when seal breeding colonies are most vulnerable to disturbance (Boren *et al.* 2002).

In Namibia, where sealing was still ongoing at the end of this study period, sealing activities at the three colonies that have been targeted since 1990 (Atlas Bay, Wolf Bay, and Cape Cross) occur on most days over a period of 4–4.5 mo leading up to the breeding season and overlapping with the start of the breeding season (Morton *et al.* 2007). It can be assumed that the disturbance associated with sealing would induce stress in the animals that survive each operation (Kirkman and Lavigne 2010), including lactating females, pups, the small proportion of females that haul out to give birth before mid-November (Rand 1967) and males that begin to haul out from mid-October to contest for territories (Rand 1967). Sealing in South Africa occurred up to 1990 when it was placed under a moratorium (Wickens *et al.* 1991), which diminished the likelihood of human disturbance sufficiently intense to induce dispersal of breeding animals in this country.

Gentry (1998) demonstrated experimentally that despite the site fidelity which is typical among pinniped species (*e.g.,* Rand 1967, Hofmeyr 2000, Pomeroy *et al.* 2000, Raum-Suryan *et al.* 2002), breeding northern fur seal (*Callorhinus ursinus*) females are flexible enough to relocate under suboptimal conditions such as when stress is induced by human disturbance. However, a condition for this behavior was the presence of a group of conspecific animals to disperse to. In the case of the Cape fur seal population, this stimulus may have been provided by colonies previously considered to be nonbreeding colonies by Oosthuizen and David (1988), such as Conception Bay, Pelican Point, Sandwich Harbour, and Cape Frio, all of which became breeding colonies during the latter half of the study period. That sealing disturbance could have influenced breeding dispersion to these and other locations is consistent with the theory that intensive, repetitive human disturbance of animals that associate humans with predation risk should result in a shifting of habitat

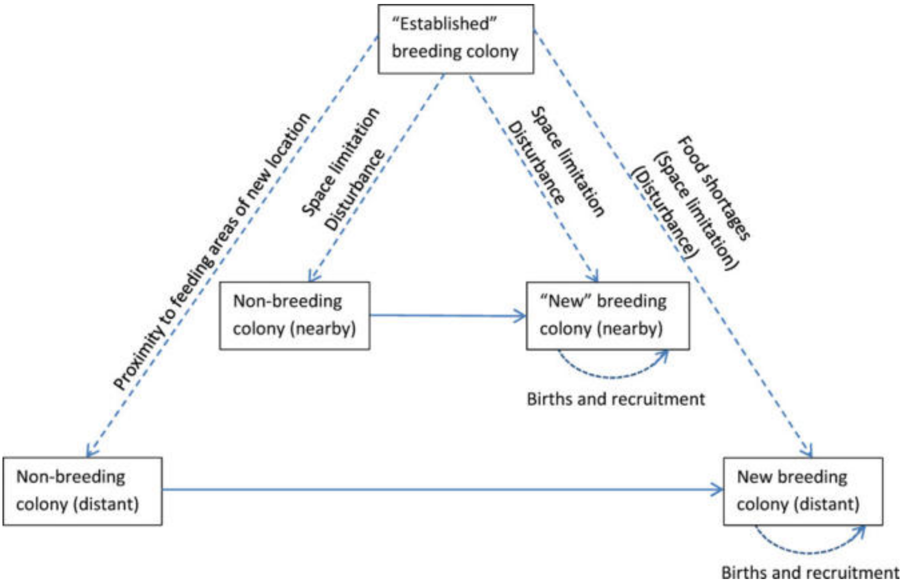

Figure 7. Hypothetical scenarios for the development of new breeding colonies. The dashed lines represent spatial shifts of animals in response to extrinsic or intrinsic pressures (which may occur singly or together); the solid lines represent a change in state of the new colony (from nonbreeding to breeding); the dotted line represents intrinsic growth of the new colony.

(Frid and Dill 2002). Females that lose their pups to the harvest and are consequently released from parental care may be more likely to disperse because they would be able to range more widely than females that lactate up until weaning.

Synthesis and Conclusions

The above mechanisms may operate in concert, including with regard to the formation of nonbreeding colonies, their transition into breeding colonies and further growth. This is illustrated in Figure 7, which depicts hypothetical scenarios for the development of new breeding colonies, in response to extrinsic or intrinsic stimuli that may occur in isolation of one another or jointly. The model is naturally a simplification; for example, an occasionally used haul-out site (Oosthuizen and David 1988), which is a possible intermediate state in the development of a new colony, is not distinguished from a nonbreeding colony in the model. In the model, a stimulus or stimuli may cause animals from an established breeding colony to haul out elsewhere. Given that breeding fur seals are likely to show fidelity to their breeding colony (Gentry 1998), the occupants at the new site are most likely to be nonbreeding animals. Such sites are likely to be in the general vicinity of the breeding colony if the stimulus was space limitation (Bradshaw *et al.* 2000, Grandi *et al.* 2008) or possibly local disturbance, but further away if related to prey.

Theoretically, transition of the new colony from a nonbreeding state to a breeding state may be brought about either by commencement of breeding by animals utilizing the location (*e.g.,* once they reach maturity), or through an influx of breeding-age animals (including pregnant females) from one or more source colonies. Given the vulnerability of pups to predation by terrestrial carnivores at many mainland locations (de Villiers and Roux 1992, Oosthuizen *et al.* 1997, Wiesel 2006), immigration of breeding-age animals may be required for some critical number of births to be attained above which the colony would be capable of increasing intrinsically at such locations, in spite of predation pressure. Such dispersal of breeding animals focused towards the new colony could be brought about by continuation of one or more negative stimuli at the source(s), or the onset of another stimulus (*e.g.,* disturbance). Examples of scenarios of stimuli operating interactively include: (1) Space limitation results in a nonbreeding colony forming on the mainland in the vicinity of an island breeding colony; following this, disturbance at the latter (*e.g.,* sealing) results in an influx of breeding animals to the mainland site. (2) Nonbreeding animals forage further afield than breeding animals, probably to avoid competition, and haul out to rest in the vicinity of their foraging grounds. Following this, prey shortages related to environmental perturbations at source cause abandonment of breeding and exodus of breeding animals to more distant foraging areas, where the aforementioned haul-outs represent potential foci for breeding in the following year. (3) Disturbance of animals at a breeding colony causes an exodus of animals, with their destination and potentially their choice of next breeding site being influenced by space limitation at nearby breeding colonies and/or greater prey availability elsewhere.

Elsewhere, large scale shifts in distribution of marine organisms of various trophic levels, ranging from planktonic organisms to top predators, have been attributed to climate change and related phenomena. These include several studies that have shown a clear and long-term shift in the distribution of planktonic groups (Reid *et al.* 1998, Beaugrand *et al.* 2002, Beagrand and Reid 2003, Richardson and Schoeman 2004). Fewer studies have also shown similar distributional changes by top predators, but in the north Atlantic, poleward range expansions have been documented for two critically endangered species, the Balearic shearwater, *Puffinus mauritanicus* (Wynn *et al.* 2007) and the leatherback turtle, *Dermochelys coriacea* (McMahon and Hays 2006); an exhaustive review of observed climate related shifts exhibited by several other species and the expected response to future climate change are reported by Parmesan (2006).

Conversely, for the Cape fur seal, the "leading edge" of the population has been shown to be at the lower-latitude margin of its distributional range. This supports the view that the responses of marine species to global changes are potentially more difficult to predict than terrestrial species given the complexities of the marine environment and food webs (Siegfried *et al.* 1990, Würsig *et al.* 2002, Harley *et al.* 2006), particularly for highly mobile animals such as marine mammals (Simmonds and Isaac 2007). In the case of the Cape fur seal (and similarly with other land-breeding marine top predators), further complexity is added by the impacts of human activities, especially the history of their past and present commercial exploitation, other exploitation of marine resources and coastal land-use within the range of the population.

The location (Northern BCLME) and timing (since the early 1990s) of the most significant changes in the Cape fur seal population in terms of both population growth and growth in the number of breeding colonies, ties in with ecosystem-scale changes that affected the distribution and abundance of prey. This indicates a bottom-up effect on the population changes mediated through prey availability which, according to Learmonth *et al.* (2006), is likely to pose the greatest threat of climate change on marine mammals. The Cape fur seal population has shown resilience to these and other changes, not only in their ability to switch prey (Mecenero *et al.* 2006*a*, *b*) and/or foraging areas (Skern-Mauritzen *et al.* 2009) but also their proven ability to colonize new areas and habitat (this study). The ability to react as they have to recent ecosystem changes apparently has been considerably influenced, and in some cases possibly even bolstered, by humans. Restriction of human access used for mining or national parks has prevented unregulated disturbance of seals in large areas of Namibia and South Africa (Rand 1972, Shaughnessy 1984). This, and possibly reductions (directly or indirectly caused by humans) in numbers of large terrestrial carnivores such as lions, *Panthera leo*, along the coastline (Rand 1972), have allowed breeding colonies to establish on the mainland including in areas that were not within the breeding range of the population historically (*i.e.*, in the northern part of Namibia). With the breeding population no longer constrained by the distribution of offshore islands as suitable breeding habitat, its capacity to respond to ecosystem-scale changes in prey availability that have pervaded in the Northern BCLME during the study period, was enhanced. Disturbance caused by commercial sealing (regulated since the early 20th century but uncontrolled before this; Wickens *et al.* 1991) at breeding colonies may have stimulated dispersal to new habitat and the establishment and growth of new breeding colonies, thereby inadvertently contributing to the population's resilience to changes in prey availability.

Management concerns regarding shifts in the distribution of the seal population include potential implications for fisheries, for other top predators and for the sealing industry. Declining trends, at least at two of the three colonies in Namibia that are subjected to sealing (Atlas Bay and Wolf Bay) may have implications for the sustainability of this industry if they are not compensated for with ameliorated catch levels. Influx of seal numbers to certain areas such as southern Angola and to the vicinity of seabird islands such as Vondeling Island, South Africa, are likely to be met with pressure to cull seals to reduce their interactions with fisheries (see Wickens *et al.* 1992) or with protected seabird species (see David *et al.* 2003).

Continued range-wide censusing of the population is recommended; this should include search effort in remote locations for new haul-outs that could develop into breeding colonies (Kirkman *et al.* 2011), and monitoring the breeding status of colonies that currently have nonbreeding status (*e.g.*, Huisamen *et al.* 2011). Interesting potential avenues for further research include comparisons of reproductive performance, phonological and behavioral attributes between the "leading edge" of the population and locations at higher latitudes. However, given the remoteness of colonies in the north of the range, considerable logistical difficulties would need to be overcome for such comparisons to be made.

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