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Recolonisation of the Robberg Peninsula (Plettenberg Bay, South Africa) by Cape fur seals

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The Cape fur seal *Arctocephalus pusillus pusillus* colony at Robberg Peninsula, Plettenberg Bay, on the south-east coast of South Africa, was driven to extinction by indiscriminate harvesting by the late 1800s. Seals only began to recolonise this site in the 1990s. This study describes the recolonisation process from 2000 to 2009, exploring both within- and between-year count data of seals using the site. Counts increased over the study period from <300 animals to >3 100. Generalised linear models indicated the importance of year and month in explaining variability in the counts. Within-year variability in the counts decreased over the study period, which may be related to an increasing proportion of resident (as opposed to transient) seals in the colony. However, the colony is currently still in a transition phase with a low ratio of breeding to non-breeding animals, based on the low numbers of pups born in the colony (currently still <100 per year). The influx of seals to the Robberg area may be associated with shifts in prey availability at the ecosystem level. The colony benefits from the protection afforded by the reserve status of the Robberg Peninsula and the existence of a marine protected area adjacent to it. However, human interference associated with fishing and/or ecotourism on the peninsula may inhibit development into a substantial breeding colony. Potential interventions for the conservation and management of this colony are discussed.

Keywords: *Arctocephalus pusillus pusillus*, breeding, counts, marine protected area, population trend

Introduction

The Cape fur seal *Arctocephalus pusillus pusillus* is the only resident pinniped on the southern African coastline (Shaughnessy 1985). The current geographical distribution of its breeding population ranges from Algoa Bay in South Africa to Baia dos Tigres in Angola (Kirkman et al. 2011). According to the Oosthuizen and David (1988) definition of a Cape fur seal breeding colony as a location where at least 100 pups per year are born regularly, there are currently 40 breeding colonies in the population (Kirkman et al. 2011). The majority of these are associated with the Benguela Current system located along the west coast of the region, with only two breeding colonies occurring to the east of Cape Agulhas, in the Agulhas Current system (Figure 1).

The current geographical distribution of the seal population differs considerably from its historical distribution, as reconstructed from the records or anecdotes of seal hunters and early travellers (e.g. Rand 1972, Shaughnessy 1982, 1984). Historically, at least nine seal colonies occurred to the east of Cape Agulhas, but most of these were hunted to extinction prior to the 20th century, including at least five colonies in Algoa Bay and another two in Plettenberg Bay (Shaughnessy 1982, Stewardson 1999). In the latter location, seals historically occurred at Beacon Island (which has since been developed and joined to the mainland) and also at Seal Point at Robberg, which forms a peninsula at the south-western end of the bay. An anecdotal record of an observation from a government official suggests that there were 3 000 seals on Robberg in about 1833 (Ross 1971). During a harvest conducted around this time (the only harvest at this colony for which a record is available) all the seals taken (n = 146) were male (Metelerkamp 1955). For this reason it has been speculated that the colony may

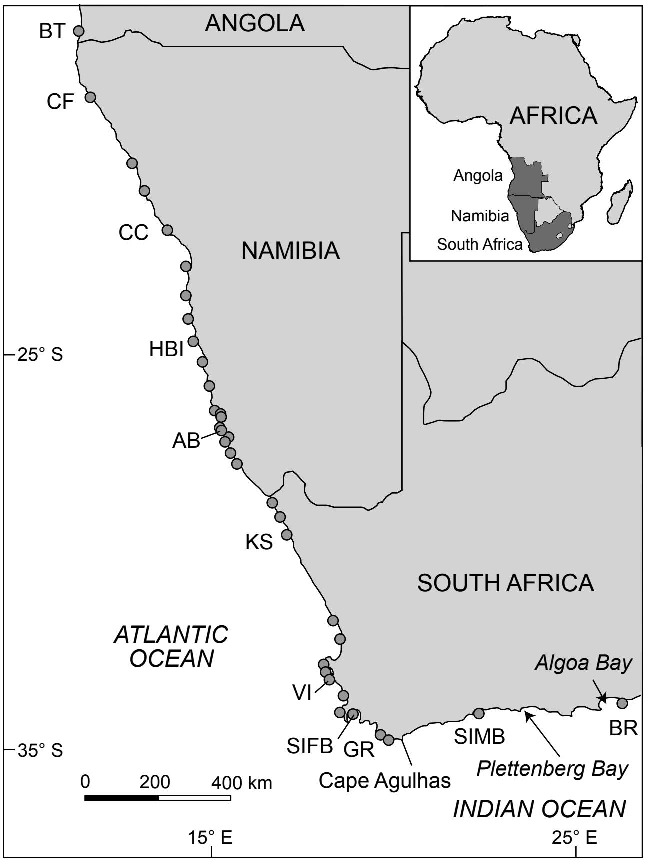

Figure 1: Map showing the range of Cape fur seal breeding colonies from Black Rocks (BR), Algoa Bay to Baia dos Tigres (BT), southern Angola. Selected breeding colonies are indicated including Seal Island in Mossel Bay (SIMB), Geyser Rock (GR), Seal Island in False Bay (SIFB), Vondeling Island (VI), Kleinsee (KS), Atlas Bay (AB), Hollam's Bird Island (HBI), Cape Cross (CC) and Cape Frio (CF)

have been a non-breeding colony (Metelerkamp 1955, Stewardson 1999), a term for colonies that are typically inhabited by immature or senescent animals, and where few births take place (Oosthuizen and David 1988, de Villiers et al. 1997). According to Ross (1971), it is likely that the colony at Robberg was extinct by 1890.

The Cape fur seal population as a whole was probably at its lowest level around the beginning of the 20th century, when numbers had been reduced to <100 000 (Shaughnessy and Butterworth 1981). However, following the introduction of protective legislation in 1893 (Best 1973), the population increased during the 20th century, even though it was still subjected to controlled harvests (Wickens et al. 1991). Since the commencement of aerial photographic surveys of the population in 1971, considerable increases in the size of the breeding population and its geographical extent have been documented (Butterworth et al. 1995, Kirkman et al. 2007, Kirkman 2010). These changes predominantly took place on the west coast of southern Africa, where the growth of several mainland colonies accounted for most of the increase in total numbers (Butterworth et al. 1995). The establishment of several new breeding colonies also saw the northernmost extent of the breeding population extend from central Namibia to northern Namibia, and recently to southern Angola. In contrast, the number of extant breeding colonies on the south coast of South Africa, and their population sizes, has remained relatively constant since 1971 (Kirkman 2010). Nevertheless, small numbers of seals returned to the Robberg Peninsula during the 1990s (Stewardson and Brett 2000). Numbers subsequently increased (Stewardson 2001) and a few newborn pups were first observed in 1996/1997 (M Brett, CapeNature, pers. comm.), leading to speculation that Robberg could eventually become a breeding colony (Stewardson 1999, Kirkman 2010).

The seal colony at Robberg was identified as a monitoring priority by the Robberg management authority (CapeNature), due to the potential for impacts of seals on local fisheries (Wickens et al. 1992) and the conservation of certain other marine top predators (Kirkman 2009), as well as the colony's ecotourism potential. This study is based on intensive monitoring of the size and distribution of the Robberg Cape fur seal colony from 2000 to 2009 and aims to describe the recolonisation process over this period, including between- and within-year temporal patterns in haulout numbers and the extent of breeding. Possible interventions for the conservation management of the colony are discussed.

Material and methods

Study site

The Robberg Peninsula is part of the Robberg Nature Reserve (Government Notice No. 1 of 1980) and is adjoined by a marine protected area (MPA), which was established during the late 1990s. The peninsula forms the south-western extremity of Plettenberg Bay, situated on the south-east coast of South Africa (Figure 1). There, the fast-flowing Agulhas Current intermittently causes inshore counter-currents and upwelling of colder water (Lutjeharms and Ansorge 2001) associated with prominent capes (Schumann et al. 1982). Rough sea conditions are generally associated with westerly cold fronts in winter (Duvenage and Morant 1984). The climate is mild (average daily maximum air temperature of 24 °C in February and average daily minimum air temperature of 10 °C in August) while rainfall occurs year-round.

Counting method

Visual counts were conducted from three vantage points on the cliff-tops above the colony. From May 2000 to December 2008 counts were carried out at least monthly (on average every 15 days) except for February 2003 and December 2005 when no counts were conducted due to a lack of personnel. Towards the end of the study period, the colony expanded (Figure 2) and it was no longer possible to count all animals from the land-based vantage points. As a result, from February 2009, bimonthly land-based counts were replaced by boat-based counts conducted every three months at a distance of about 40 m from the high water mark.

Each count was carried out by three observers and the mean was taken to represent the number of seals present in the colony. Only seals present on land were counted, despite the fact that there were often large numbers in the

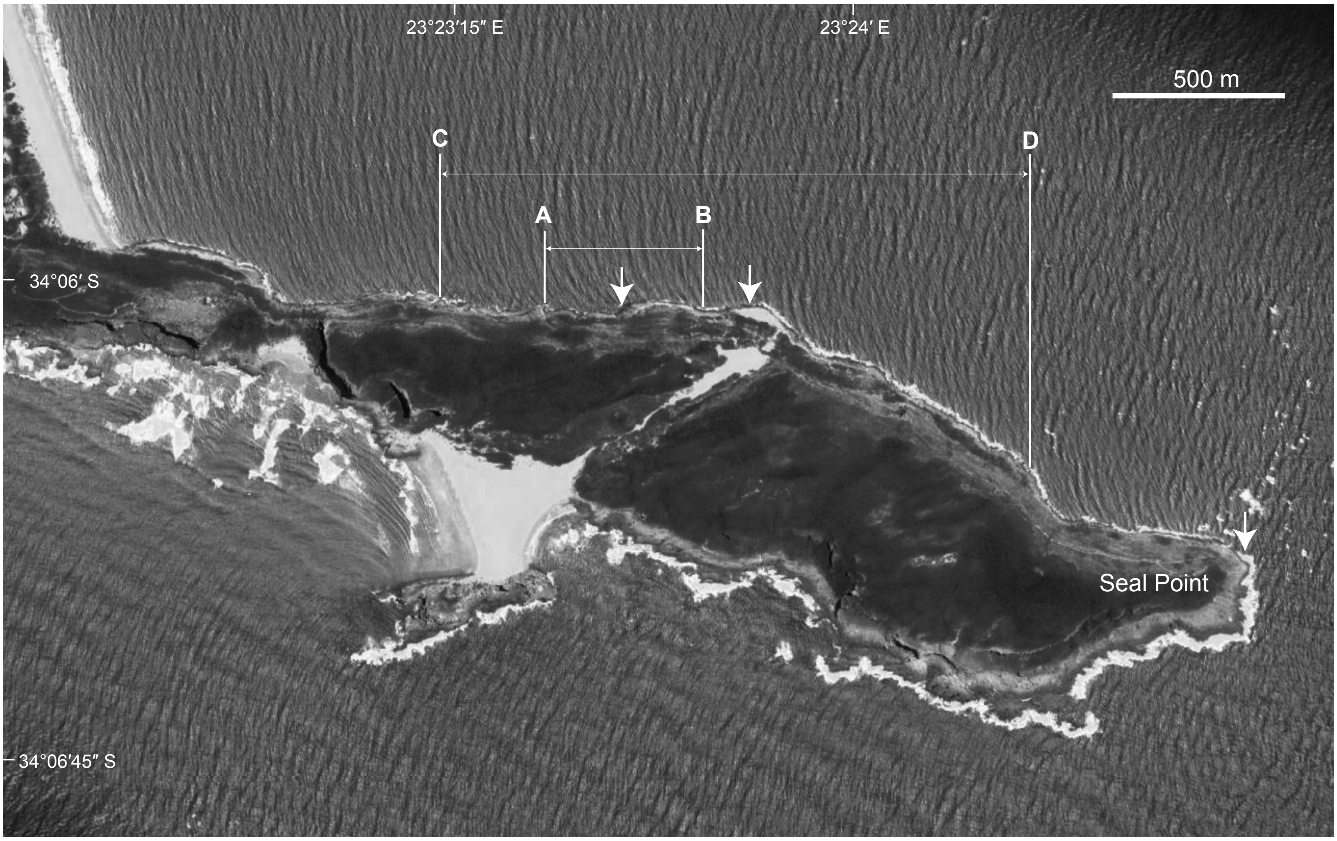

Figure 2: Google Earth image (http://earth.google.com/) of the Robberg Peninsula showing the extent of the seal colony along the coast at the beginning of the study (between A and B) and after 2008 (between C and D). The most suitable access points for seals on the north face of the peninsula are marked with arrows

water in close proximity to the haulout sites. Counts were generally carried out between 09:00 and 11:00 (Figure 3a). Global positioning system (GPS) readings to record the extent of the haulout area were taken on 23 June 2000 and again on 13 August 2009. Pups, defined as animals in their first year of life, were distinguished from older animals based on their small size and the morphometric and colour descriptions of Rand (1956), and were counted separately. No further separation into different age- or sex-classes (e.g. subadults or adults, males or females) was made. As from February 2009, counts of pups were not possible because their small size and the oblique angle of the boat-based observations made detecting them difficult.

Data analysis

Analyses were conducted using generalised linear models (GLMs) in the freely available statistical software package R, version 2.11.0 (R Development Core Team 2009) with the packages 'nlme' (Pinheiro and Bates 2011), 'lmtest' (Hothorn et al. 2010) and 'car' (Fox and Weisberg 2011) incorporated. GLMs are an extension of standard linear models in that they allow the response data to follow a distribution from the 'exponential family', which includes normal, binomial, gamma and Poisson distributions. The Poisson distribution, which assumes that the variance is equal to the mean, is often used when modelling count data (McCullagh and Nelder 1989), and such models have frequently been used to estimate the trend and abundance of seal populations (e.g. Frost et al. 1999, Small et al. 2003, Mathews et al. 2011). Therefore, a GLM with a Poisson distribution and a log link function was initially used to describe the relationship between seal numbers at Robberg and several explanatory variables, with the counts as the response variable. Only the land-based count data (2000–2008) were considered in the GLM. Counts subsequent to 2008 were not included in this analysis to avoid potential bias associated with using different count techniques. The following explanatory variables were considered for inclusion in the model: (1) year; (2) month; (3) time of day (Figure 3a), converted to number of hours after first light (Figure 3b) to account for variation among seasons; (4) wave height; (5) air temperature; (6) sea surface temperature (SST); and (7) lunar phase. Lunar phase was described using two categories, the bright moon (from first quarter to last quarter) and dark moon (from last quarter to first quarter). A series of models were run either with year as a continuous or a categorical variable. Time of year was represented by one of the following: (a) the four seasons as a categorical variable; (b) the 12 months as a categorical variable; (c) month as a continuous variable; and (d) month transformed to trigonometric functions using a Fourier transformation, so that the variable

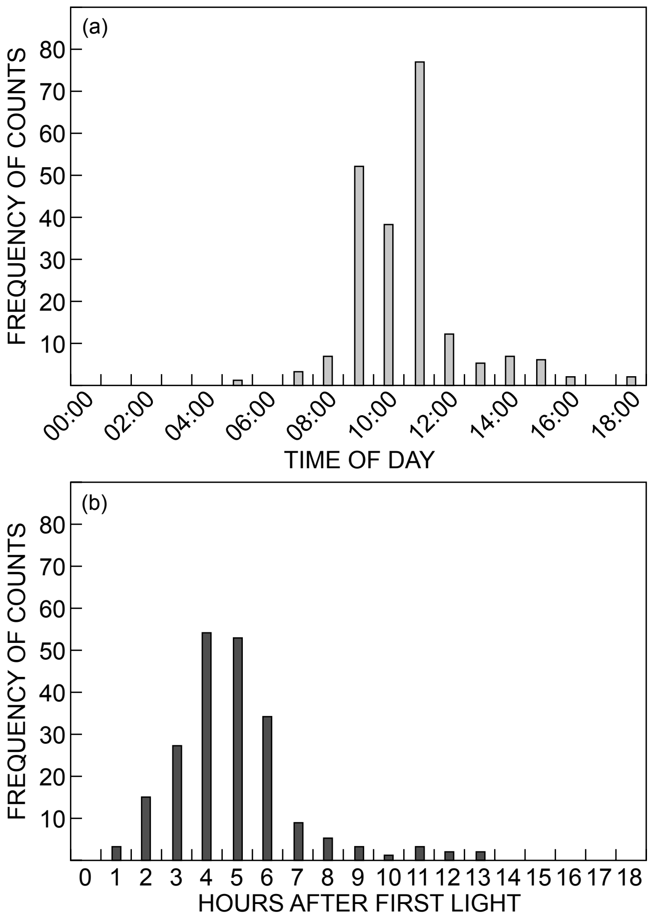

Figure 3: Frequency of seal counts carried out at (a) different times of day and (b) times of day converted to number of hours after first light

was independent of year-end and the last month of the year was continuous with the first month of the next year (Underhill et al. 1992). Aikaike's information criterion (AIC) was used to choose the most parsimonious model under the various alternatives for year and time of year. On this basis, year and month were finally included in the model as categorical variables along with variables 3–7. The only interaction term that was considered was year–month.

We examined whether the assumption of equivalence between the variance and the mean held true by specifying a quasi-Poisson distribution as the error structure in the model. The resulting dispersion parameter was considerably greater than one (ρ = 120). This indicated that the errors were overdispersed and not consistent with the assumption of a Poisson distribution. Therefore, a quasi-Poisson distribution, which assumes that the variance is proportional rather than equal to the mean to account for the overdispersion in model residuals, was specified (Hardin and Hilbe 2003, Faraway 2006). Comparing AIC scores is not a valid way of choosing between quasi-Poisson GLMs. Instead automated, backwards stepwise deletion of variables was carried out based on *p*-values of the analysis of variance (ANOVA) tests with the significance level set at 0.05. This was done to eliminate explanatory variables that did not significantly influence the response variable, and to determine the most parsimonious final model. A 'pseudo' R^2, an adjusted R^2 measure for overdispersed Poisson models (Heinzl and Mittlböck 2003), was estimated for the model as

$$\frac{(D_N - D_R)}{D_N}$$

where D_N is the null deviance of the model and D_R is the residual deviance.

Results

From 2000 to 2009, 212 land-based and three boat-based counts of the seal colony were conducted. There was a clear increasing trend in seal numbers over the study period (Figure 4). Following stepwise deletion of explanatory variables from the full model, only year, month and the interaction between these variables were found to significantly influence the response (Table 1). Under this formulation of the model, these variables accounted for 75% of the variation in the land-based seal counts as indicated by the value of the 'pseudo' R^2 (D_N = 56 429, df = 210; D_R = 14 467, df = 109). The model had the following structure in terms of the response variable:

$$y_{ij} = X_i + W_j + X_i W_j + \varepsilon_{ij}$$

$$\varepsilon_{ij} \sim \text{qpois}(\mu_{ij}, \rho\mu_{ij})$$

where X_i is the value of the *i*-th year, W_j is the value of the *j*-th month and ε is the error, which was assumed to have a quasi-Poisson distribution; μ is the expected mean value of the response under the model and ρ is the dispersion parameter.

The fact that the interaction between year and month (Table 1) was retained in the model as significant reflects the differences in the trend of monthly seal counts between the years. Plots of the within-year counts fitted with linear trend lines (Figure 5) indicated that there was greater stability in the within-year counts towards the end of the land-based count series (2006–2008), compared with earlier years. Seal numbers increased significantly over the time-series (Table 1), but it is evident that the increase was not consistent over time (Figure 6). Using the land-based count data, the model indicated an initial rapid increase in numbers of around 19% per year (95% CI = 12–26%) between 2000 and 2003, followed by a downward fluctuation (−22%) in 2004, and a further steady increase of approximately 12% per year since 2006 (7–17%).

Corresponding with the overall increase in seal numbers, the number of pups counted in the colony also increased from 1 in 2000 to 36 in 2007 (Figure 4a), according to the land-based counts. In 2005 and 2008, the land-based counts could be compared with aerial census counts conducted by the former Marine and Coastal Management (MCM), Department of Environmental Affairs and Tourism (now Oceans and Coasts, Department of Environmental Affairs). These counts were carried out near the end of the seal breeding season (c. 20 December) in these years, as

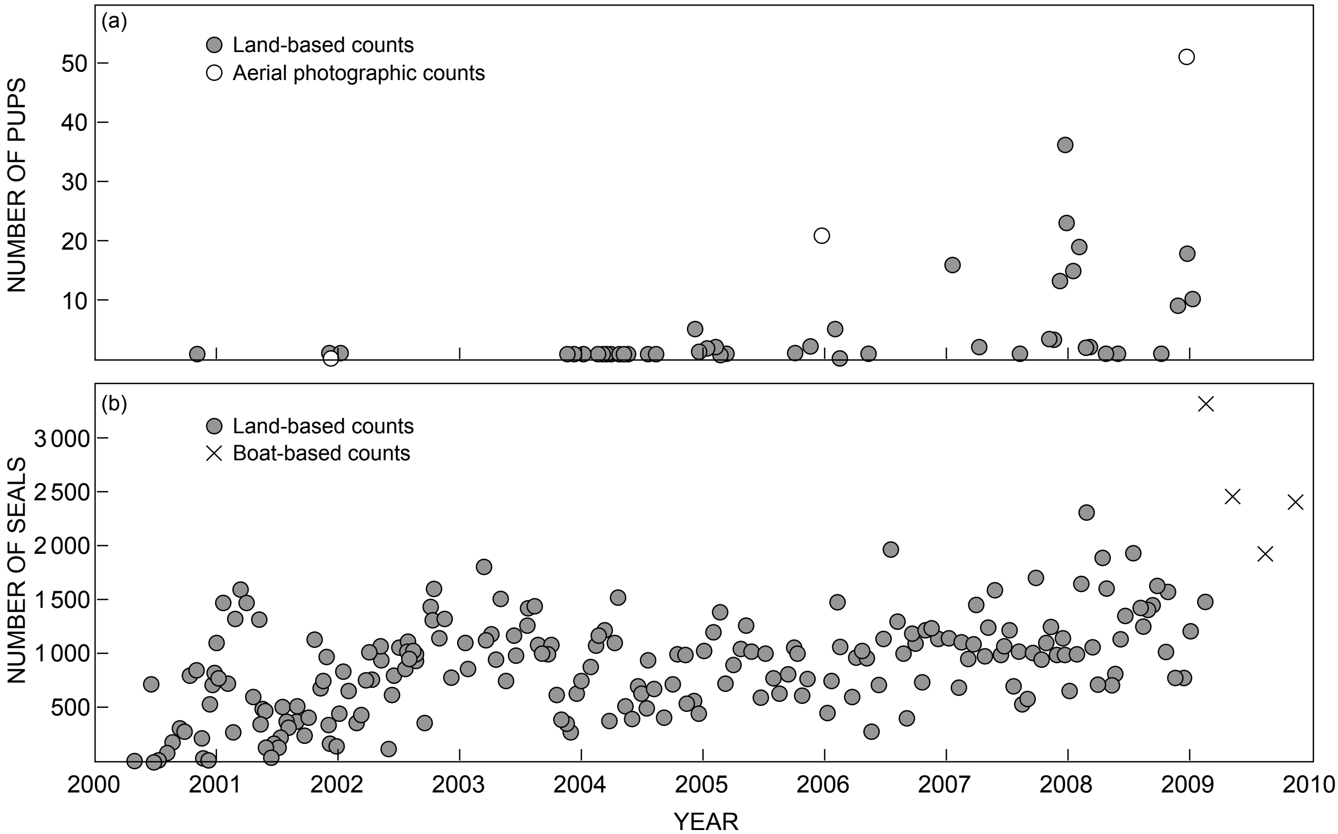

Figure 4: Counts of (a) seal pups and (b) seals excluding pups at Robberg from 2000 to 2009

Table 1: Analysis of variance (Type II) results for explanatory variables in the final generalised linear model, following automated backwards stepwise deletion of insignificant variables

Variable	Sum of squares	df	*F*-value	*p*-value
Year	15 595.0	8	16.0	<0.001
Month	2 994.8	11	2.2	0.018
Year × Month	20 183.8	82	2.0	<0.001
Residuals	13 321.4	109		

part of MCM's region-wide survey of the seal population. The land-based pup counts in 2005 and 2008 were 2 and 19 animals, which were lower than the corresponding aerial census counts by 90% (n = 21) and 63% (n = 51) respectively (Figure 4a).

Between 2000 and 2007, Cape fur seals hauled out along a limited section of the north-facing shore of Robberg (between points A and B in Figure 2) and then expanded east and west in 2007 (between C and D in Figure 2). Currently, the length of the colony along the shore of the peninsula is 1.7 km; at its widest, it is approximately 30 m from the high-water mark. After changing to boat-based counts from 2009 onwards, the entire length of the colony could be observed. This, together with continued growth of the colony, is likely to have accounted for the relatively high counts of 2009 (Figure 4b). Land-based counts carried out following the longitudinal expansion of the colony are likely are likely to have underestimated the total number of seals present compared with the early years in the study when the entire colony was visible. However, judging from the upward trend over the entire period (Figure 6), the effect of this bias on the model predictions is likely to have been negligible.

Discussion

This study described the process of recolonisation of the Robberg Peninsula by Cape fur seals between 2000 and 2009, exploring both between- and within-year count data of seals and the extent of breeding at the site. The counts only represented seals ashore and did not include animals at sea at the time. Therefore, the trends that are reported here are relative and cannot be used to assess absolute abundance of seals in this colony.

A comparison of the land-based counts of seal pups in the Robberg colony in 2005 and 2008, and the aerial photographic census counts conducted by MCM in those years (Figure 4a), suggested that pups were under-represented in land-based counts. The aerial photographic

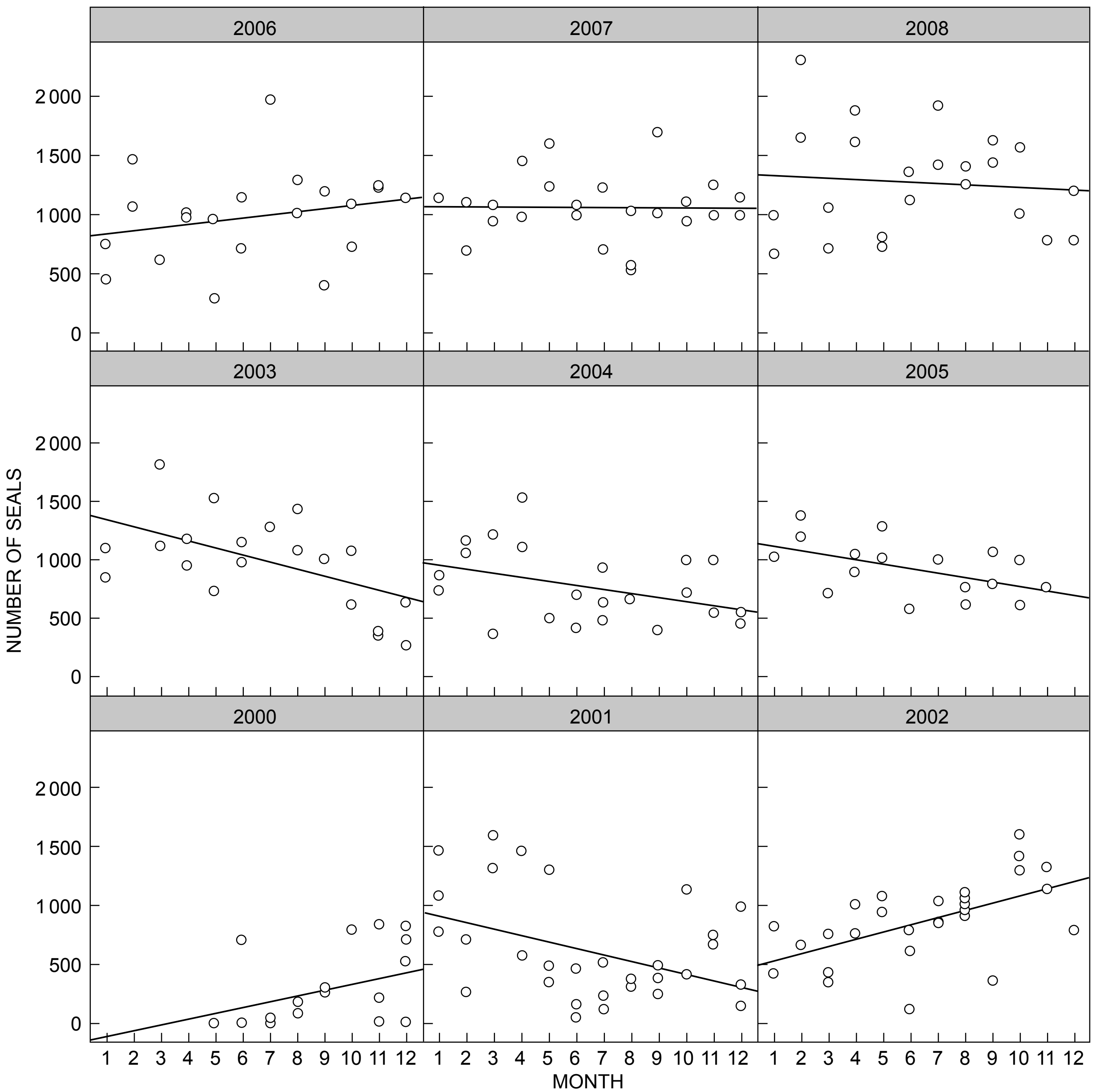

Figure 5: Numbers of seals counted throughout each year (months 1–12) from 2000 to 2008 (land-based counts only). Linear trend lines are included to illustrate the different numerical patterns between years

count is expected to be the more accurate because it is easier to count animals in a photographic snapshot than to count live animals by eye (Kirkman 2007). Moreover, the entire colony would have been covered from a near-vertical angle during the aerial census, whereas during the land-based counts the areas of the colony farthest from the vantage points were viewed from a relatively oblique angle (approx. 45°). Given their small size after birth, some pups are likely to be hidden from view by larger animals or boulders during land-based counts.

Based on the most recent aerial photographic census count, the colony would not be classified as a breeding colony (100 pups or more; Oosthuizen and David 1988). The non-breeding status of the colony is also highlighted by the very small ratio of pups to older animals at the end of the breeding season (1:44 in 2005 and 1:25 in 2008). An approximately even ratio between pups and adults would be expected if the main function of the colony was breeding, as adult females and their newborn pups would make up the bulk of the seal numbers at the colony. Considering

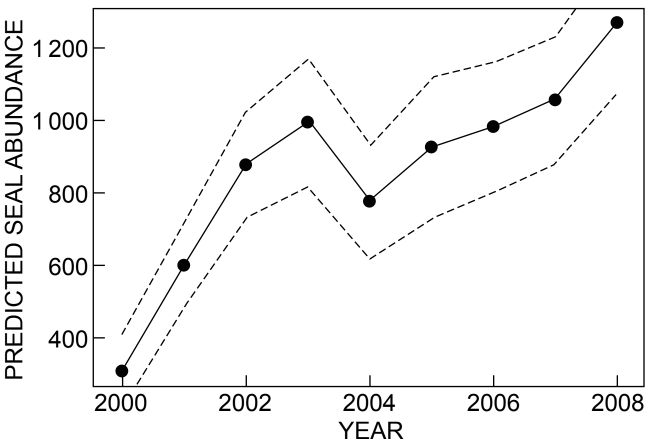

Figure 6: Yearly mean numbers of seals at the Robberg seal colony between 2000 and 2008 (land-based counts only) as predicted by the generalised linear model. Dashed lines show 95% confidence intervals

that reliable counts of pups cannot be obtained during the boat-based counts (which replaced the land-based counts after 2008), aerial censuses of the colony are recommended for future assessment of the breeding status of the colony.

When compared to the final three years of land-based counts, higher within- and between-year variation was evident in seal numbers during the earlier years of the study period, particularly from 2000 to 2003 (Figure 5). We postulate that the greater variation during earlier years was symptomatic of the early developmental stages of the colony. In these years, the composition of the colony at any time is likely to have been characterised by transient seals, with numbers possibly dependent on prey availability in the area. Non-breeding seals are not obligated to return to a central place — unlike lactating females — so it might be expected that their numbers would be more sensitive to fluctuations in local prey availability. In this regard, it is possible that the downward trend in seal numbers between 2003 and 2004 may have been caused by local reductions in prey availability. However, as the colony grows, it would be expected that the number of resident seals in the colony would increase in proportion to temporary visitors, therefore stabilising overall numbers. The small number of pups born at the colony together with the relatively high rates of increase in total seal numbers from 2000 to 2004 (19% per annum) and again after 2004 (12% per annum) indicate that continuing immigration is primarily responsible for the colony's growth.

Elsewhere, weather or sea conditions (Hofmeyr et al. 2006), lunar phase (Trillmich and Mohren 1981), and time of day (Rand 1959, Gentry 1973) have been shown to affect diurnal or day-to-day variation in numbers of fur seals in colonies. The lack of importance accorded to any of these by the GLM in this study may have been due to the temporal resolution of the land-based counts, which were on average 15 days apart (SD 8.2). However, the broad-scale temporal trends of the colony were well explained by year and month (75% of variability).

Results of region-wide (South Africa, Namibia and Angola) monitoring of the seal population using aerial photographic surveys since the 1970s has brought to light considerable changes in the distribution and abundance of the wider population (Kirkman 2010). This includes the development of 17 new breeding colonies, all on the west coast of southern Africa. These changes have been linked to the effects of environmental changes on prey availability but also to the lack of human interference on the coastlines of these areas, due to inaccessibility or restrictions on access (e.g. diamond mining areas, national parks), that could otherwise prevent the successful establishment of seal colonies. In comparison, the number of seals and seal colonies on the south coast of South Africa (between Cape Town and Port Elizabeth) has remained stable until now. The colony at Robberg is the first new colony to develop on the South Coast since the 1970s. Until the establishment of this colony, the c. 400 km stretch of coastline between Seal Island near Mossel Bay and Black Rocks in Algoa Bay (Figure 1) was by far the longest stretch of coastline within the current breeding range of Cape fur seals that was devoid of a seal colony (Kirkman 2010).

Development of non-breeding colonies and their transition to breeding colonies have been shown to be a characteristic of the 'recolonisation' phase (Roux 1987) in otariid populations recovering from past over-exploitation (e.g. Oosthuizen and David 1988, Bradshaw et al. 2000, Grandi et al. 2008). The establishment has been attributed to saturation of space-at-source breeding colonies (e.g. Bradshaw et al. 2000, Grandi et al. 2008), but another possible cause includes the convenience of haulout sites with respect to feeding grounds. In the case of Robberg, the well-documented shift in the geographical distribution of certain prey resources such as sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* from the west towards the east Agulhas Bank (i.e. east of Cape Agulhas) (e.g. van der Lingen et al. 2006) may have increased the availability of prey in the Robberg area and influenced the influx of seals. Southward and eastward shifts in the geographical distribution of some other top predator species (e.g. Cape gannet *Morus capensis*, swift tern *Sterna bergii* and Cape cormorant *Phalacrocorax capensis*) along South Africa's coastline have been associated with these changes (Crawford et al. 2008a, 2008b).

Fur seals are gregarious and require groups of conspecific animals for breeding (David 1989, Gentry 1998). Once there is a nucleus of breeding animals, the size of the colony may grow rapidly. Groups may surpass the maximum intrinsic rate of increase (approximately 17%, Payne 1977) if the site becomes a focal point for dispersal for breeding age animals from other crowded colonies. An example of a colony that has shown this kind of rapid increase is Vondeling Island (Figure 1), a former guano island on the west coast of South Africa, which has been recolonised by seals since 2000 at a growth rate of more than 100% per annum (Kirkman 2010). However, the area of the Robberg Peninsula that is currently inhabited by seals (Figure 2) may not be ideally suited for the development of a breeding colony. There is limited space between cliffs and the sea (~30 m at most) and there are only two suitable access points in the existing colony where seals can move safely between the sea and land. This would most likely limit the number of territories that can be established there by breeding males, because the prime territories would be established at the access points and movement to other areas behind the prime territories would be difficult due to territorial aggression.

According to historical records (Metelerkamp 1955), seals previously occurred at the rocky shelf at the point of Robberg Peninsula, some 800 m to the east of the current colony, which was duly named Seal Point (Figure 2). To date, seals have not recolonised this location, which is more accessible and more spacious than the current colony and appears to be more suitable for breeding. A popular hiking trail traverses this area and it is also a popular recreational fishing area. Therefore human disturbance associated with these activities may until now have affected the choice of habitat by seals on the peninsula; the current location of the colony is inaccessible to tourists and fishers. Such disturbance is likely to be largely incidental, but in the case of fishers it may also be deliberate, considering the potential for increasing conflict between seals and fishers in the area (JH, unpublished data) because many fishers perceive seals to be competitors (Meÿer et al. 1992, Wickens et al. 1992). Management interventions that may encourage recolonisation of the point area and further growth of the colony could therefore include re-routing of the hiking trail and declaring the area at the point a no-take area for fishers. The latter is realistic in terms of the zoning policy for MPAs, though it is likely to be met with resistance by fishers whom generally laid the blame for declining linefish catches in the vicinity of Plettenberg Bay area on the increase of seals (King 2005, Smith 2005).

With or without human intervention, the continued growth of the Cape fur seal colony at Robberg Peninsula seems likely, based on the population trajectory over the past decade. This will have repercussions at various levels, ranging from the conservation status of the species in the region through to the socio-economic implications, with ecotourism benefits on the one hand and perceived competition with fisheries on the other. In terms of competition with fisheries, it is important that the degree of overlap between the diet of Cape fur seals at the Robberg colony and fish stocks targeted, both recreationally and commercially, is assessed to ensure the availability of robust data when decisions regarding the management and conservation of this colony need to be made.

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References

Best PB. 1973. Seals and sealing in South and South West Africa. *The South African Shipping News and Fishing Industry Review* 28: 49–57.

Bradshaw CJA, Lalas C, Thompson CM. 2000. Clustering of colonies in an expanding population of New Zealand fur seals (*Arctocephalus forsteri*). *Journal of Zoology* [London] 250: 105–112.

Butterworth DS, Punt AE, Oosthuizen WH, Wickens PA. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 3. Modelling the dynamics of the Cape fur seal *Arctocephalus pusillus pusillus. South African Journal of Marine Science* 16: 161–183.

Crawford RJM, Sabarros PS, Fairweather T, Underhill LG, Wolfaardt AC. 2008a. Implications for seabirds off South Africa of a long-term change in the distribution of sardine. *African Journal of Marine Science* 30: 177–184.

Crawford RJM, Tree AJ, Whittington PA, Visagie J, Upfold L, Roxburg KJ, Martin AP, Dyer BM. 2008b. Recent distributional changes of seabirds in South Africa: is climate having an impact? *African Journal of Marine Science* 30: 189–193.

David JHM. 1989. Seals. In: Payne AIL, Crawford RJM (eds), *Oceans of life*. Cape Town: Vlaeberg Publishers. pp 288–302.

de Villiers DJ, Oosthuizen WH, Roux J-P, Kotze PGH. 1997. Population structure of a non-breeding colony of the Cape fur seal *Arctocephalus pusillus pusillus* at Cape Frio, Namibia. *South African Journal of Marine Science* 18: 295–298.

Duvenage IR, Morant PD. 1984. CSIR research report. Estuaries of the Cape. Part 2. Synopsis of available information on individual systems. Report Number 31. Keurbooms System (CMS 19). Piesang (CMS 18). Stellenbosch: Council for Scientific and Industrial Research.

Faraway RJJ. 2006. *Extending the linear model*. New York: Taylor and Francis.

Fox J, Weisberg S. 2011. Car: companion to applied regression. R package version 2.0–10. Available at http://CRAN.R-project.org/package=car [accessed 20 April 2011].

Frost KJ, Lowry LF, Ver Hoef JM. 1999. Monitoring the trend of harbor seals in Prince William Sound, Alaska, after the Exxon Valdez oil spill. *Marine Mammal Science* 15: 494–506.

Gentry RL. 1973. Thermoregulatory behaviour of eared seals. *Behaviour* 46: 73–93.

Gentry R. 1998. *Behavior and ecology of the northern fur seal*. Princeton: Princeton University Press.

Grandi MF, Dans SL, Crespo EA. 2008. Social composition and spatial distribution of colonies in an expanding population of South American sea lions. *Journal of Mammalogy* 89: 1218–1228.

Hardin JW, Hilbe JM. 2003. *Generalized estimating equations*. New York: Chapman & Hall/CRC.

Heinzl H, Mittlböck M. 2003. Pseudo R-squared measures for Poisson regression models with over- or underdispersion. *Computational Statistics & Data Analysis* 44: 253–271.

Hofmeyr GJG, Bester MN, Makhado AB, Pistorius PA. 2006. Population changes in Subantarctic and Antarctic fur seals at Marion Island. *South African Journal of Wildlife Research* 36: 55–68.

Hothorn T, Zeileis A, Millo G, Mitchell D. 2010. lmtest: Available at http://CRAN.R-project.org/package=lmtest [accessed 20 April 2011].

King CM. 2005. Towards a new approach for coastal governance with an assessment of the Plettenberg bay shore-based linefishery. MSc thesis, Rhodes University, South Africa.

Kirkman SP. 2007. Recommendations for a regional monitoring programme for Cape fur seals in the BCLME. In: Kirkman SP (ed.), *Final report of the BCLME (Benguela Current Large Marine Ecosystem) Project on top predators as biological indicators of ecosystem change in the BCLME*. Cape Town: Avian Demography Unit, University of Cape Town. pp 367–371.

Kirkman SP. 2009. Evaluating seal-seabird interactions in southern Africa: a critical review. *African Journal of Marine Science* 31: 1–18.

Kirkman SP. 2010. The Cape fur seal: monitoring and management in the Benguela Current ecosystem. PhD thesis, University of Cape Town, South Africa.

Kirkman SP, Oosthuizen WH, Meÿer MA, Kotze PGH, Roux J-P, Underhill LG. 2007. 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. *African Journal of Marine Science* 29: 161–176.

Kirkman SP, Oosthuizen WH, Meÿer MA, Seakamela SM, Underhill LG. 2011. Prioritising range-wide scientific monitoring of the Cape fur seal in southern Africa. In: Kirkman S, Elwen SH, Pistorius PA, Thornton M, Weir CR (eds), *Conservation biology of marine mammals in the southern African subregion. African Journal of Marine Science* 33: 495–509.

Lutjeharms JRE, Ansorge IJ. 2001. The Agulhas return current. *Journal of Marine Systems* 30: 115–138.

McCullagh P, Nelder JA (eds). 1989. *Generalized linear models*. London, UK: Chapman & Hall.

Mathews EA, Womble JN, Pendleton GW, Jemison LA, Maniscalco JM, Streveler G. 2011. Population growth and colonization of Steller sea lions in the Glacier Bay region of southeastern Alaska: 1970s–2009. *Marine Mammal Science* 27: 852–880.

Metelerkamp S (ed.). 1955. *George Rex of Knysna*. Cape Town: Timmins.

Meÿer MA, Kotze PGH, Brill GW. 1992. Consumption of catch and interference with linefishing by South-African (Cape) fur seals *Arctocephalus pusillus pusillus*. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds), *Benguela trophic functioning. South African Journal of Marine Science* 12: 835–842.

Oosthuizen WH, David JHM. 1988. Non-breeding colonies of the South African (Cape) fur seal in southern Africa. *Investigational Report, Sea Fisheries Research Institute, South Africa* 132: 1–17.

Payne MR. 1977. Growth of a fur seal population. *Philosophical Transactions of the Royal Society B* [London] 279: 67–79.

Pinheiro J, Bates D. 2011. nlme: linear and nonlinear mixed effects models. R package version 3.1-100. Available at http://CRAN.R-project.org/package=nlme [accessed 20 April 2011].

R Development Core Team. 2009. R: A language and environment for statistical computing. Vienna: R. Foundation for Statistical Computing. Available at http://www.R-project.org [accessed 15 December 2009].

Rand RW. 1956. The Cape fur seal *Arctocephalus pusillus* (Schreber). Its general characteristics and moult. *Investigational Report, Division of Sea Fisheries, South Africa* 21: 1–52.

Rand RW. 1959. The Cape fur seal (*Arctocephalus pusillus pusillus*). Distribution, abundance and feeding habits off the southwestern coast of the Cape Province. *Investigational Report, Sea Fisheries, South Africa* 34: 1–75.

Rand RW. 1972. The Cape fur seal *Arctocephalus pusillus*. 4. Estimates of population size. *Investigational Report, Sea Fisheries, South Africa* 89: 1–28.

Ross GJB. 1971. Notes on seals and sealing in the Eastern Cape. *The Eastern Cape Naturalist* 44: 6–8.

Roux J-P. 1987. Recolonisation processes in the Subantarctic fur seal, *Arctocephalus tropicalis*, on Amsterdam Island. In: Croxall JP, Gentry RL (eds), *Status, biology, and ecology of fur seals: proceedings of an international symposium and workshop, Cambridge, England, 23–27 April 1984*. NOAA Technical Report NMFS 51. Seattle, Washington: NOAA. pp 189–194.

Schumann EH, Perrins LA, Hunter IT. 1982. Upwelling along the South Coast of the Cape Province, South Africa. *South African Journal of Science* 78: 238–242.

Shaughnessy PD. 1982. The status of seals in South Africa and South West Africa. *Mammals of the seas. FAO Fisheries Series* 5: 383–410.

Shaughnessy PD. 1984. Historical population levels of seals and seabirds on islands off southern Africa, with special reference to Seal Island, False Bay. *Investigational Report, Sea Fisheries Research Institute, South Africa* 127.

Shaughnessy PD. 1985. Interactions between fisheries and Cape fur seals in southern Africa. In: Beddington JR, Beverton RJH, Lavigne DM (eds), *Marine mammals and fisheries*. London: George Allen and Unwin. pp 119–134.

Shaughnessy PD, Butterworth DS. 1981. Historical trends in the population size of the Cape fur seal (*Arctocephalus pusillus*). In: Chapman JA, Pursley D (eds), *The worldwide furbearer conference proceedings*. Virginia: RR Donnelley and Sons Co. pp 1305–1327.

Small RJ, Pendleton GW, Pitcher KW. 2003. Trends in abundance of Alaska harbor seals, 1983–2002. *Marine Mammal Science* 19: 344–362.

Smith MKS. 2005. Towards a new approach for coastal governance with an assessment of the Plettenberg Bay nearshore linefisheries. MSc thesis, Rhodes University, South Africa.

Stewardson CL. 1999. The impact of the fur seal industry on the distribution and abundance of Cape fur seals *Arctocephalus pusillus pusillus* on the Eastern Cape coast of South Africa. *Transactions of the Royal Society of South Africa* 54: 217–245.

Stewardson CL. 2001. Biology and conservation of the Cape (South African) fur seal. PhD thesis, Australian National University, Australia.

Stewardson CL, Brett M. 2000. Aggressive behaviour of an adult male Cape fur seal (*Arctocephalus pusillus pusillus*) towards a great white shark (*Carcharodon carcharias*). *African Zoology* 35: 147–150.

Trillmich F, Mohren W. 1981. Effects of the lunar cycle on the Galapagos fur seal, *Arctocephalus galepagoensis*. *Oecologia* 48: 85–92.

Underhill LG, Prys-Jones RP, Harrison JA, Martinez P. 1992. Seasonal patterns of occurrence of Palaearctic migrants in southern Africa using atlas data. *Ibis* 134: 99–108.

van der Lingen CD, Shannon LJ, Cury P, Kreiner A, Moloney CL, Roux J-P, Vaz-Velho F. 2006. Resource and ecosystem variability, including regime shifts, in the Benguela Current System. In: Shannon V, Hempel G, Malanotte-Rizzoli P, Moloney CL, Woods J (eds), *Benguela: predicting a large marine ecosystem*. *Large marine ecosystems* 14. Amsterdam: Elsevier. pp 147–185.

Wickens PA, David JHM, Shelton PA, Field JG. 1991. Trends in harvests and pup numbers of the South African fur seal: implications for management. *South African Journal of Marine Science* 11: 307–326.

Wickens PA, Japp DW, Shelton PA, Kriel F, Goosen PC, Rose B, Augustyn CJ, Bross CAR, Penney AJ, Krohn RG. 1992. Seals and fisheries in South Africa – competition and conflict. In: Payne AIL, Brink KH, Mann KH, Hilborn R (eds), *Benguela trophic functioning*. *South African Journal of Marine Science* 12: 773–789.