THE CAPE FUR SEAL: MONITORING AND MANAGEMENT IN THE BENGUELA CURRENT ECOSYSTEM

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ABSTRACT

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Title: The Cape fur seal: monitoring and management in the Benguela Current Ecosystem

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At the root of this thesis was the Benguela Current Large Marine Ecosystem (BCLME) Programme's project "Top Predators as Biological Indicators of Ecosystem Change in the BCLME" (LMR/EAF/03/02). The objectives of this project were to assess the utility of top predators as biological indicators of ecosystem change in the Benguela Current Ecosystem, and implement an appropriate, integrated, system-wide monitoring programme based on top predators, to support ecosystem-based management in the Benguela Current Ecosystem. In line with these objectives, this study included the following: Investigation of relevant time series of information on seals; Contrasting of alternative approaches for the analysis of long term information; Description of changes in the distribution and abundance of the seal population, with discussion of intrinsic and extrinsic factors potentially underlying these changes; Consideration of management implications of observed changes in the seal population, including mitigation of detrimental effects on other species; Investigation of behavioural responses of Cape fur seals to environmental variability, using satellite telemetry for the first time; Assessment of detrimental effects of certain research on seals and implications for the interpretation of data; Recommendations for seal monitoring taking into account monitoring priorities that have been identified for the region; Details of appropriate techniques for seal monitoring in the region; Proposed future research of relevance to improving monitoring protocols and assisting the interpretation of monitoring outcomes.

Analysis of a time series of aerial photographic censuses of the seal population indicated that the size of the population in the last decade was similar to its size in 1992, the time of the last comprehensive assessment of the population's size and growth. This was despite the establishment and growth of several new breeding colonies especially since the 1980s. Fluctuating rates of change and numerical declines at several breeding colonies, particularly in Namibia during the latter part of the study period (since c. 1992), suggested that extrinsic factors played a large role in levelling the population size. Taking into consideration known changes in the distribution and abundance of prey in the Benguela Current Ecosystem, seal foraging behaviour in the northern part of this ecosystem and geographical gradients with regard to the changes in distribution and abundance of the seal population, these observed patterns appeared to be mainly attributable to the effects of environmental variability on prey availability.

Flexibility in foraging behaviour and site fidelity in response to variable feeding conditions or other determinants of the population's dynamics (e.g. human interference), may be the key to the persistence of the population at its current level, despite adverse environmental conditions and human pressures. A consequence of this was the establishment of new breeding colonies that have apparently allowed the seal population to track changes in the distribution of prey or escape human interference, or both. At least at some locations however, colony density or human interference may have played a role in these changes. Human disturbance within a seal breeding colony was shown to cause medium- to long-term dispersal of animals from the disturbed areas, therefore extensive human interference such as seal harvesting at colonies may cause re-location of animals to other areas, possibly contributing to the establishment and growth of new colonies.

To further enhance understanding of the drivers of seal population dynamics, including being able to distinguish between human- and climate-related effects on trends in population size and distribution, region-wide monitoring of other population parameters to complement continued aerial census monitoring, was recommended. These included key performance (e.g. growth) and behavioural (e.g. foraging ecology) attributes of seals that can be related to environmental or other biological variables. Implications for management of changes in the seal population were also considered, especially effects of seals on endemic seabird populations. Preventative or mitigating measures to address seal expansion into seabird breeding colonies were recommended.

Keywords: abundance, *Arctocephalus pusillus pusillus*, Benguela, breeding, distribution, ecosystem, management, monitoring, Namibia, population, South Africa

LAYOUT, DETAILS OF PUBLICATIONS, ACKNOWLEDGEMENT OF INPUTS FROM CONTRIBUTORS

This thesis consists of seven chapters, in addition to the introduction and synthesis, and an annex. Four of these are data chapters, two are review-style chapters which carry recommendations for research or management, and one is a short communication. Six of the seven chapters are written as manuscripts for submission to peer-reviewed scientific journals and the seventh (Chapter 8) is written as a chapter for a published contract report. The annex is linked to Chapter 8 and was published in the same contract report. In keeping with the style for manuscript submissions, references, tables, figures and where applicable, appendices, are included at the end of each chapter. As a result, some repetition between chapters is inevitable, but I have tried to keep this to a minimum. My own contributions to each chapter, and where applicable, details of publication and involvement of co-authors and/or other contributors are specified below:

Chapter 2: Making sense of censuses and dealing with missing data: trends in pup counts of Cape fur seal for the period 1971–2003

Details of publication:

Kirkman SP, Oosthuizen WH, Meÿer MA, Kotze PGH, Roux J-P, Underhill LG (2007) Making sense out of censuses and dealing with missing data: trends in pup counts of Cape fur seals between 1972–2004. *African Journal of Marine Science* 29: 161–176

My input:

I conceived of and researched the article, and was responsible for the analysis, interpretation, the bulk of the writing and incorporating comments from co-authors. I also participated in the 2001 aerial census.

Input of co-authors:

WHO and JPR made contributions to the interpretation and writing up; MAM and PGHK were responsible for conducting the aerial censuses, processing aerial photographs and enumerating seals; LGU provided supervision, especially with regard to statistics.

Other contributions:

J David, G Hofmeyr, D de Villiers, S Swanson and D Reynolds all participated in past aerial censuses and/or assisted with processing of photographs and enumeration of seals. L Drapeau provided assistance with GIS. Comments received from the reviewers of the paper after it was submitted were incorporated.

Chapter 3: A critical assessment of seal-seabird interactions in southern Africa, reflecting on past versus present population size of the Cape fur seal

Details of publication:

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

My input:

I conceived, researched and wrote the article.

Other Contributions:

WH Oosthuizen, MA Meÿer and PGH Kotze provided useful information, S Mecenero and WHO made helpful comments on an earlier version of the manuscript and comments received from the reviewers of the paper after it was submitted were incorporated.

Chapter 4: Spatio-temporal effects of research-related disturbance at a Cape fur seal breeding colony

Details of publication:

Kirkman SP, Louw G, Skrypzeck H, Underhill LG. *South African Journal of Wildlife Research* (to be submitted)

My input:

I conceived of the study and helped research it, supervised the enumeration of seals on aerial photographs and statistical analysis, interpreted the results and wrote the article.

Input of co-authors:

GL enumerated seals on aerial photographs, assisted with researching the article, conducted statistical analysis under my supervision and contributed to the writing of the article. HS and LG also contributed to the writing of the article.

Other Contributions:

Osbourne, K Seaward and H Blom enumerated seals on aerial photographs. S Mecenero and M de Villiers provided comments on an earlier version.

Chapter 5: Do inter-colony differences in Cape fur seal foraging behaviour reflect large-scale differences in the northern Benguela Current Ecosystem

Details of publication:

Skern-Mauritzen M, Kirkman SP, Olsen EJS, Bjørge A, Drapeau L, Mëyer MA, Roux J-P, Swanson S, Oosthuizen WH (2009) Do inter-colony differences in Cape fur seal foraging behaviour reflect large-scale changes in the northern Benguela ecosystem? *African Journal of Marine Science* 31: 399–408

My input:

I contributed to the planning and logistics of the study, participated in fieldwork and workshops, and co-wrote the paper.

Input of co-authors:

MS-M co-wrote the paper. MS-M, EJSO, MAM, J-PR, SS and WHO participated in fieldwork. MS-M, LD, EJSO, MAM, J-PR, AB and WHO contributed to analysis of telemetry data and interpretation of results during workshops. WHO, MAM and AB contributed to planning and logistics.

Other contributions:

N Mukapuli and T Kleophas assisted in the field. NM contributed to logistics and in workshops. Comments received from the reviewers of the paper after it was submitted were incorporated.

Chapter 6: Distributional shifts of the dynamic Cape fur seal breeding population in southern Africa, based on aerial censuses (1971–2009)

Details of publication:

Kirkman SP, Yemane D, Oosthuizen WH, Meÿer MA, Kotze PGH, Skrypzeck H, Roux J-P, Underhill LG. *Canadian Journal of Zoology* (to be submitted)

My input:

I conceived of and researched the paper, and was responsible for the analysis, interpretation and writing up. I participated in the 2001 aerial census, and I helped to supervise enumeration of seals on aerial photographs since 2005.

Input of co-authors:

MAM, PGHK, HS and J-PR all were instrumental in past aerial censuses. MAM was responsible for the supervision of the processing of photographs and enumeration of seal on them. DY assisted with regard to running analyses in the statistical programme ‘R’. LGU and WHO contributed to the writing up of the paper.

Other contributions:

J David, G Hofmeyr, J-P Roux, D Villiers, S Swanson, L Staverees, D Reynolds, D Anders, S McCue, S Maduray, M Seakamela, S Singh, K Pillay, S Osbourne, K Seaward, N Mukapuli, T Kleophas, all participated in past aerial censuses and/or assisted with processing of photographs and enumeration of seals on them.

Chapter 7: An unusual nursing interaction between Cape fur seals

Details of publication:

Kirkman SP (2010) An unusual nursing interaction between two adult Cape fur seals. *African Journal of Marine Science* 32 in press

My input:

I made the behavioural observation documented in the article and researched and wrote the article.

Other Contributions:

WH Oosthuizen, MA Meÿer and PGH Kotze provided insight and advice. Comments received from the reviewers of the paper after it was submitted were incorporated.

Chapter 8: Recommendations for a regional monitoring programme for Cape fur seals in the Benguela Current Ecosystem

Details of publication:

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*. Avian Demography Unit, Cape Town, pp 367–371

My input:

I researched and wrote the article.

Other Contributions:

J-P Roux and WH Oosthuizen provided helpful comments and suggestions.

Annex 1: Manual of methods for basic monitoring of Cape fur seals in the Benguela Current Ecosystem

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Kirkman SP (ed.) (2007) Annex 2. Manual of methods for monitoring 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*. Avian Demography Unit, Cape Town, pp 1–44

My input:

I researched and compiled the three chapters of the manual.

Other Contributions:

Input to the section on diet monitoring was provided by S Mecenero, J-P Roux, MA Meÿer and PGH Kotze. MAM and PGHK provided input to the section on estimating pup numbers, and J-PR and MAM to the section on mass at birth and pup growth.

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CHAPTER 1

Introduction

Taxonomy and biology

The Cape fur seal *Arctocephalus pusillus pusillus* (also known as the South African fur seal) belongs to the family Otariidae, which includes fur seals and sea lions (Bonner 1994, Brunner 2004). Fur seals are distinguished from sea lions mainly by the presence of abundant under-fur, which is lacking in the latter. There are two fur seal genera, namely *Arctocephalus* and the monotypic *Callorhinus*, the former consisting of eight species, with the Cape fur seal and the Australian fur seal *A. p. doriferus* sharing subspecies status (Bonner 1981, Riedmann 1990). The remaining seven species of *Arctocephalus* are: the South American fur seal *A. australis*, the Juan Fernandez fur seal *A. philippi*, the Galapagos fur seal *A. galapagoensis*, the Guadalupe fur seal *A. townsendi*, the New Zealand fur seal *A. forsteri*, the subantarctic fur seal *A. tropicalis* and the Antarctic fur seal *A. gazella*. With the exception of *A. townsendi*, all *Arctocephalus* species occur in the southern hemisphere, hence the vernacular term "southern fur seals" (Bonner 1981).

In terms of appearance, social behaviour, reproduction and ecological role, southern fur seal species are remarkably similar to each other (Gentry and Kooyman 1986). All are sexually dimorphic in body size (males outweigh females by 2- to 4-fold, depending on species), and have a polygynous mating system characterised by territorial aggression on the part of adult males. In the Cape fur seal, for example, harem sizes are usually between 10 and 30 females per territorial bull during the breeding season (Wickens and York 1997). Females give birth to a single pup (twin births are extremely rare) after a gestation period of about 12 months (including a four month period of delayed implantation). The natal fur of pups is nearly always black or dark brown in colour, in contrast to adults which are typically a grizzled dark-grey brown dorsally, shading to lighter beneath (only the male *A. tropicalis* is clearly bi-coloured) (Bonner 1981).

Breeding is synchronous; in the Cape fur seal the breeding season is from November to early January each year, with a peak in births during the first half of December (David 1987a, de Villiers and Roux 1992). Post-parturient adult females remain with their pups for a few days after giving birth, during which period they mate, before they depart to sea to feed (Gentry and Kooyman 1986). From then until weaning, the females intersperse foraging trips to sea with suckling bouts ashore. The duration of the lactation period varies between species, from approximately four months in the Antarctic fur seal to two years or more in the Galapagos fur seal (Gentry and Kooyman 1986, Wickens and York 1997). In the Cape fur seal, the length of the lactation period is 8–11 months, with weaning taking place between July and October (Rand 1955, David and Rand 1986). After first parturition, which occurs at age 3–5 years, fur seal females may give birth each year until death (Wickens and York 1997).

In terms of trophic relationships, all fur seal species fulfil the role of top predators in the marine ecosystem that they inhabit. They generally appear to be opportunistic hunters, feeding predominantly on teleost fish, cephalopods or crustaceans (David 1987b, Harcourt *et al*. 2002, Kirkman *et al*. 2000, Mecenero 2005). Fur seals in turn constitute prey of killer whales *Orcinus orca* (Newman and Springer 2008, pers. obs.) and large sharks such as the great white shark *Carcharodon carcharias* (Martin *et al.* 2005, pers. obs.). Fur seal species that breed at mainland locations are also at risk from terrestrial predators, such as brown hyenas *Hyaena brunnea* and black-backed jackals *Canis mesomelas* in the case of the Cape fur seal (Oosthuizen *et al*. 1997, Wiesel 2006, pers. obs.).

Trends in distribution and abundance

Cape fur seals occur along the southern and western coasts of southern Africa (Figure 1), where they currently breed at numerous island and mainland locations. It was thought that historically, breeding colonies of this sub-species occurred almost exclusively at island locations, with terrestrial predators including early hunter-gatherers generally preventing viable breeding colonies from occurring on the mainland (Rand 1972). However, uncontrolled seal harvesting (sealing) that took place between the 17th and 19th centuries following the arrival of Europeans in the region led to the extirpation of seal breeding colonies at several islands (Rand 1952, 1972, Shaughnessy 1984, David and van Sittert 2008). By the beginning of the 20th century when the population was probably at its most reduced level, numbers are thought to have been less than 100 000 individuals (Shaughnessy and Butterworth 1981) and breeding colonies had disappeared from at least 23 coastal islands (Best and Shaughnessy 1979, Shaughnessy 1982).

The remaining seals were generally restricted to small islands and rocky outcrops which were inaccessible or unprofitable for sealers or guano collectors to exploit (Rand 1952, Shaughnessy 1984). Despite the introduction of control measures on sealing around the beginning of the 20th century, re-colonisation of many of their former island breeding colonies was inhibited by human activities, mostly related to the exploitation of seabird products (e.g. guano, eggs) (Shaughnessy 1984). However, around the middle of the 20th century, breeding colonies were established at mainland locations, including at Kleinsee in South Africa and at Atlas Bay and Wolf Bay in Namibia (Rand 1972). The growth in seal numbers at these colonies and at Cape Cross, a mainland colony in Namibia which existed before the 20th century, was largely accountable for a recovery in seal numbers during the 20th century, with numbers estimated at 1.7 million animals (excluding pups of the year) in 1992 (Butterworth *et al*. 1995). There has been speculation as to whether the current size of the seal population exceeds the pre-sealing population size, which is unknown (e.g. Crawford and Robinson 1990, Makhado *et al.* 2006).

Environment and prey

The greater part of the Cape fur seal population (> 90 %) occurs along the coast of Namibia and the west coast of South Africa (David 1989) (Figure 1). This region corresponds with the cold, nutrient-rich Benguela Current Ecosystem, also referred to as the Benguela Upwelling System. The Benguela Current Ecosystem is one of the four major upwelling systems in the world (Bakun 1996) and although productive, is characteristically variable at different spatial and temporal scales (Shannon *et al*. 1988, Shannon and Jarre-Teichmann 1999).

Prevailing winds in the Benguela Current Ecosystem are determined by the high-pressure system in the South Atlantic ocean, atmospheric pressure over the mainland and low-pressure systems related to westerly winds south of South Africa; where the wind is strongest and the continental shelf deepest and narrowest, upwelling centres occur (Shannon 1989, Bakun 1996), most notably at Cape Columbine, Lüderitz and Cape Frio (Figure 1). The degree of upwelling is dependent on the prevailing wind conditions, the angle of the coast to the prevailing wind direction, and the depth and width of the continental shelf (Shannon 1989). The upwelling centre around Lüderitz is the most intense in the world (Bakun 1996) and the resulting cold sea temperatures in this area form a barrier to the movement of several marine faunal species, that effectively divides the Benguela Current Ecosystem into northern and southern components (Shannon 1985).

At least three features of the Benguela Current Ecosystem contribute to the existence of large populations of land-breeding top predators, including the Cape fur seal, in this region. Firstly, the productivity of the marine environment supports abundant fish stocks that in turn can sustain abundant top predators (van der Lingen *et al*. 2006). Secondly, apart from generating ocean productivity through coastal upwelling, the prevailing winds have a cooling effect that provides benign climatic conditions for land breeding marine predators (including seals) to breed under (Peard 2007). Thirdly, several islands occur off the coast in the region, providing breeding habitat that is isolated from terrestrial predators (Shaughnessy 1984, Williams *et al*. 2000). Although seal colonies are currently extinct at many (c. 20) of these islands, restriction of human access and possibly depletion of terrestrial predators along large strips of coastline in South Africa and Namibia, including reserves and areas zoned for diamond mining, have provided alternative breeding habitat to seals (Rand 1972, Shaughnessy 1984).

Cape fur seals feed predominantly over the continental shelf (David 1987b, Chapter 5). The bulk of the Cape fur seal diet is comprised of teleost fish, mainly pelagic shoaling fish such as sardine *Sardinops sagax*, anchovy *Engraulis encrasicolus*, round herring (redeye) *Etrumeus whiteheadii*, Cape horse mackerel *Trachurus trachurus capensis* and juvenile hake *Merluccius* spp. (Shaughnessy 1985, David 1987b, Mecenero *et al*. 2006a). All the above are targeted by commercial fisheries but non-commercial fish species including goby *Sufflogobius bibarbatus* and lantern fish *Lampanyctodes hectoris* also feature prominently in the seal diet in some areas (Mecenero *et al*. 2006a). West coast rock lobster *Palinurus delagoae* and cephalopods especially the chokka squid *Loligo vulgaris reynaudii* also feature in the diet, especially on the west and south coasts of South Africa, respectively (David 1987b, Lipinski and David 1990). Cape fur seals also prey on certain seabird species, with and increasing frequency of attacks being recorded since the 1980s (David *et al*. 2003, Makhado *et al*. 2006).

South Africa and Namibia's sardine stocks collapsed in the 1960s and 1970s, respectively, due to over-exploitation, but whereas this species has generally remained in a depleted state in Namibian waters, the South African stock subsequently recovered to record biomass levels in the early 2000s (Griffiths *et al*. 2005, van der Lingen *et al*. 2005). However, since the 1990s there have been marked eastward shifts in the geographical distributions of the sardine (Fairweather *et al.* 2006), anchovy (Roy *et al.* 2007) and west coast rock lobster (Cockcroft *et al.* 2008) stocks in South Africa, with consequences for commercial fisheries (van der Lingen *et al*. 2006) and for locally breeding seabirds that are dependent on these prey (Crawford *et al*. 2008a, 2008b). It has been speculated that the progressive shifts of these prey stocks away from the west coast of South Africa, where the bulk of the country's seal population occurs (David 1989), may have resulted in nutritional stress to seals in this area (Makhado *et al*. 2006).

In Namibia, adverse environmental conditions in the 1990s (Gammelsrød *et al.* 1998), exacerbated by overfishing (Boyer and Hampton 2001), resulted in severe depletion of prey resources for seals, including hake, horse mackerel, anchovy and sardine, through death, poor recruitment and dispersal. These prey groups have generally remained in a depleted state especially in southern and central Namibia (Cury and Shannon 2004, van der Lingen *et al.* 2006) with severe implications for commercial fisheries and for top predators including seals and several seabird species in the area (Crawford *et al*. 2006, Kemper 2006, van der Lingen *et al*. 2006). However, northward shifts in the distributions of some prey (e.g. horse mackerel) associated with the prevailing unfavourable conditions have effectively increased the availability of prey for seals in the north of Namibia and southern Angola (Axelsen *et al.* 2004, Mecenero *et al.* 2007, van der Lingen *et al*. 2006).

Research, monitoring, management

The recovery of Cape fur seal numbers during the 20th century has been largely attributed to the imposition of legal controls on seal harvesting around the beginning of the 20th century (David 1989). However, it was not until the early 1970s that sustained research effort dedicated to assessing seal numbers for the purpose of informing decisions on sustainable harvesting quotas, was initiated. Two approaches were used, namely tag-recapture studies of pups in their natal colonies and censusing of new born pups present in breeding colonies at the end of the breeding season using aerial photography (Shaughnessy 1987, 1993). For practical reasons (explained in Annex 1, Section 2), aerial photography became the *modus operandi* for obtaining coverage of pup numbers for the entire population. Pups are targeted during the censuses, *inter alia* because they are the only demographic category that is all confined to land (at least during their first month of life) and because their numbers can be used to infer adult population size subject to certain assumptions (Wickens and Shelton 1992), or provide input for population growth models (e.g. Butterworth *et al.* 1995).

Whereas seal harvesting has continued in Namibia up to the present (Kirkman and Lavigne 2010), it was discontinued in South Africa in 1990 (Wickens *et al.* 1991). Despite this, census coverage of seal colonies over the entire region was continued. During the course of the time series, the emphasis of the research goals expanded to include assessment of interactions between the seal population and commercial fisheries (Butterworth and Harwood 1991), for which numerical estimates of the population were a prerequisite (i.e. for consumption estimates). To this end, seals were also systematically sampled (lethally) at sea during dedicated research surveys conducted in several years between 1974 and 2001 (David 1987b, Kirkman 2007a). The purpose of these surveys was to collect data on diet composition (from stomach samples) and data relevant to the estimation of vital population parameters such as age structure and reproductive rates.

Following the cessation of seal harvesting in South Africa in 1990, there was increased pressure to cull seal numbers to alleviate perceived competitive effects of seals on commercial fisheries (Wickens *et al*. 1992). A modelling study that took the above diet and population information into consideration to assess the seal-fishery relationship and assist management decisions, was commissioned by the South African government in the early 1990s. The model outcomes emphasised that the effects of reducing a top predator on fishery yields are not intuitively obvious on account of the complex and dynamic nature of the marine food web, and may in fact be counter-productive (Punt and Butterworth 1995). On this advice, the government has subsequently resisted calls by fisheries to reduce seal numbers (Cochrane *et al.* 2004).

The growth of the Ecosystem Approach to Fisheries (EAF) concept (Cochrane *et al.* 2004), especially since 2000, provided seal research in the region with renewed impetus and justified the continuation (and improvement) of region-wide research and monitoring of the population. Changes in numbers, distribution or other characteristics of marine top predators are frequently symptomatic of changes occurring at lower trophic levels, such as may be caused by effects of over-fishing or other environmental (e.g. climatic) changes (Diamond and Devlin 2003, Reid *et al.* 2005). Therefore, there is increasing recognition that information on top predators, if they are well monitored, may provide useful indicators of ecosystem health or changes in marine resources (Montevecchi and Myers 1995, Boyd and Murray 2001). The use of indicators is informative for EAF, towards which fisheries management in the region has been shifting (Cochrane *et al.* 2004, Roux and Shannon 2004).

Also relevant to EAF is *inter alia* the consideration of interactions between fisheries and non target species (including top predators) that are detrimental to either or both, interspecific interactions to the detriment of one or more species of conservation concern, and the management or mitigation of these interactions where necessary (Kirkman 2007a). Whereas the former has for long been a prominent topic of research and debate in the region (e.g. Butterworth *et al*. 1988 Wickens *et al*. 1992), harmful effects (predation, competition for breeding space) of seals on seabird species that are both endemic to the region and under conservation threat is a relatively recent concern (du Toit *et al.* 2003). The seabird species concerned include the Cape gannet *Morus capensis*, the African penguin *Spheniscus demersus* and cormorants

Phalacrocorax spp., all of which, like the Cape fur seal, have geographical distributions that traverse national boundaries (transboundary distributions) (Kemper *et al.* 2007). Thus, with several fish stocks of economic importance and top predator populations shared between nation states of the Benguela Current Ecosystem, regional co-ordination of research, monitoring and management is essential for EAF to be effective in the region. The need for transboundary co-operation in the region has been further underscored by recent wide-scale changes in the distribution and abundance of several fish stocks and top predator populations (including Cape fur seals), attributable to environmental variability and over-fishing (Gammelsrød *et al.* 1998, Boyer and Hampton 2001) with severe implications for species conservation and human livelihoods (van der Lingen *et al.* 2006).

This study

The Benguela Current Large Marine Ecosystem (BCLME) Programme, a multi-sectoral, regional initiative between Angola, Namibia and South Africa, co-ordinated numerous projects during the past decade that fitted with its stated objective of facilitating the integrated management, sustainable development and protection of the Benguela Current Ecosystem. One of these projects “Top Predators as Biological Indicators of Ecosystem Change in the BCLME” (LMR/EAF/03/02) (Kirkman 2007a) was at the root of this thesis. The stated objectives of LMR/EAF/03/02 were “to assess the utility of top predators as biological indicators of ecosystem change in the Benguela Current Ecosystem”, and “to implement an appropriate, integrated, system-wide monitoring programme [based on top predators] to support sustainable management of the BCLME.”

In fulfilling these objectives, several tasks were conducted under the project, including *inter alia* (1) Review and analysis of existing time series of information on land-breeding top predators in the region; (2) Assessment of linkages between the time series and comparative information (e.g. environmental and fisheries data), giving consideration to means of mitigating adverse influences; (3) Defining of objectives for an ecosystem monitoring programme based on top predators and identification of parameters required to attain these objectives; (4) Testing the potential for use of satellite transmitters in an ecosystem monitoring programme; (5) Description of appropriate methods for monitoring, and (6) Formulation of recommendations for an integrated ecosystem monitoring programme in the region based on land-breeding top predators, including the initiation of new time series where appropriate and guidelines for interpreting data from the monitoring programme.

Reliable long term time series of information depends upon continuity in data collection methods. Complicating factors in this regard include effects of technological advances in monitoring equipment and techniques on time series information and, with particular relevance to the seal time series, effects of shifting management and research objectives (as discussed above) on the collection of data. The former is the subject of another study (recommended during this study). With regard to the latter, an example was the aforementioned at-sea sampling of seal diet, which was implemented to investigate biological interactions between seals and fisheries. The usefulness of this data series for assessing medium to long term temporal patterns and assessing relatedness of the data to other variables was limited due to a lack of continuity in the sampling design with regard to the timing and location of surveys (Kirkman 2007a). Furthermore, due to practical problems associated with obtaining replicated, random samples using this approach, the cost of ship's time, and ethical concerns regarding the necessity for lethal sampling (Butterworth and Harwood 1991, Pierce and Boyle 1991), this time series was discontinued. It has been superseded by the more cost-effective and replicable technique of faecal (scat) sampling in seal colonies for monitoring dietary changes.

Systematic scat sampling was initiated in South Africa only after I commenced with this thesis. A longer diet time series exists for Namibian colonies (initiated in the early 1990s) but an assessment of these data was the subject of another thesis (Mecenero 2005, Mecenero *et al*. 2005, 2006a, 2006b, 2006c, 2007). Therefore, time series of diet information for seals was not included in this thesis, although procedures for scat sampling and analysis were considered in Annex 1 (section 4). Three of the chapters in this thesis were based on the aerial photographic time series of seal pup numbers, which is the longest and only current time series that can be seen as representative of the entire range of the population. These and the other chapters are discussed below.

In Chapter 2 "Making sense of censuses and dealing with missing data: trends in pup counts of Cape fur seal for the period 1971–2003", pup counts were used to determine trends in abundance of the seal population, especially since 1992, the last data point of the previous population assessment (Butterworth *et al*. 1995). Part of the chapter was dedicated to addressing the issue of missing data, which was a recurring problem in the census time series. More specifically, where numerical trends were determined from collective pup counts of colonies per year, complete aerial coverage in each census year was frequently not achieved due to weather conditions, logistical problems or other reasons. In years with missing data it was necessary to fill the gaps with proxy values in order to avoid underestimates of total numbers. Previous studies have dealt with this problem in various ways, but none have attempted to empirically assess the reliability of their approach for estimating missing data values. In this study, I assessed the accuracy shown by four different methods in approximating the correct values of all the available counts in the pup count time series (of all known breeding colonies), with a view to determining the best-suited approach. Once this was achieved and missing data values were inferred accordingly, the trends in pup numbers of the whole population and various sub-sets of the population were investigated, and the resulting patterns were interpreted and discussed *inter alia* in the light of known changes in the Benguela Current Ecosystem. The assessment was based on all the censuses up to 2003 because subsequent counts were incomplete at the time of writing this chapter, and was published as Kirkman *et al*. (2007).

Chapter 3 "A critical assessment of seal-seabird interactions in southern Africa, reflecting on past versus present population size of the Cape fur seal" addressed an issue which is relevant to ecosystem-based management (includes EAF) and which was one of the monitoring priorities identified for the region (Kirkman 2007a). The chapter critically reviewed the interpretation of anecdotes and facts that have been presented in various reports and publications concerning seal-seabird interactions, and the scientific basis for some of the justificatory arguments that have been posited regarding the management of this problem. The emphasis was on the direct impacts of seals on seabirds including predation and competition for breeding space, rather than indirect effects such as competition for prey. The chapter, which concluded with some management recommendations for mitigation of detrimental effects on seabirds, was published as Kirkman (2009).

In Chapter 4 "Spatio-temporal effects of research-related disturbance at a Cape fur seal breeding colony", aerial photographic records of a seal breeding colony were used to conduct a retrospective experiment to determine whether investigator disturbance in demarcated study sites affected the distribution of animals in the colony. Implications for the representativeness of data collected from disturbed experimental sites were discussed in the light of the results.

In Chapter 5 "Do inter-colony differences in Cape fur seal foraging behaviour reflect large-scale differences in the northern Benguela Current Ecosystem", satellite telemetry was used to investigate foraging behaviour of Cape fur seals, comparing between animals of different sex and between animals tagged at three different colonies in Namibia. The colonies were in geographically distinct areas with one colony centrally situated and one each to the north and south of this one. It was expected that seal foraging behaviour would reflect a gradient of deteriorating feeding conditions from north to south, based on the current understanding of the state of the environment and prey availability in the northern Benguela Current Ecosystem.

The main goal of Chapter 6 “Distributional shifts of the Cape fur seal breeding population in southern Africa, based on aerial censuses (1971–2009)” was to report on changes in the spatial distribution of the seal breeding population since the initiation of aerial photographic censuses in the 1970s. To this end, numerical trends were quantified for individual colonies, including breeding colonies that existed at the start of the time series and breeding colonies that were established subsequently. A quantile regression approach was used to estimate trends in pup numbers that were used as proxies for numbers of breeding animals at colonies. Six extra census years, including two years with “comprehensive” censuses of the populations (censuses during which at least two thirds of all breeding colonies were covered), were available for this assessment compared with Chapter 3, which did not assess trends for individual colonies. In assessing numerical patterns in space and time, I also attempted to gain some insight into processes underlying the distributional shifts in the breeding population and the establishment of new colonies, by discussing the results in the context of relevant ecological theory. Finally, I discussed implications of the observed geographical shifts in the seal population for its research and management.

Chapter 7 “An unusual nursing interaction between Cape fur seals” recorded a previously undocumented behavioural interaction between Cape fur seals and discussed the event in the light of behavioural theory. The importance of being alert to rare and/or new behaviour in wildlife populations and of documenting such observations, given the current unprecedented rate of global environmental changes, was emphasised. This chapter is currently in press (Kirkman 2010).

Chapter 8 “Recommendations for a regional monitoring programme for Cape fur seals in the Benguela Current Ecosystem” (published as Kirkman 2007b) discussed useful seal monitoring parameters and tools in the context of priorities that have been identified for an ecosystem monitoring programme in the Benguela Current Ecosystem. The need for an integrated approach incorporating demographic, performance and behavioural attributes of seals and for co-ordination of monitoring effort and standardising of sampling techniques, data management software and procedures, was emphasised.

Annex 1 “Manual of methods for basic monitoring of Cape fur seals in the Benguela Current Ecosystem” presents procedures for the three essential monitoring requirements that were identified for a “basic” seal monitoring programme in Benguela Current Ecosystem in Chapter 8. Besides drawing on information from the literature, knowledge and firsthand experience of various researchers in the field was incorporated and wherever possible, a theoretical background was provided with regard to sampling design and the analysis and interpretation of data. Emphasis was placed on the need for carefully designed studies that have the various scales of spatial and temporal variability in mind, standardization of techniques and sampling dates to facilitate comparisons, and suitable sample sizes. Where relevant, requirements for further research to strengthen monitoring protocols, was highlighted. The manual was published in Kirkman (2007c).

Annex 2: “Publications by SP Kirkman relating to seals”. My first research papers relating to seals were published in 1999–2000 and were based on participation in research expeditions to Marion and Bouvet Islands. This annex provides a record of my research activity in a broader field of seal biology than that confined to this thesis.

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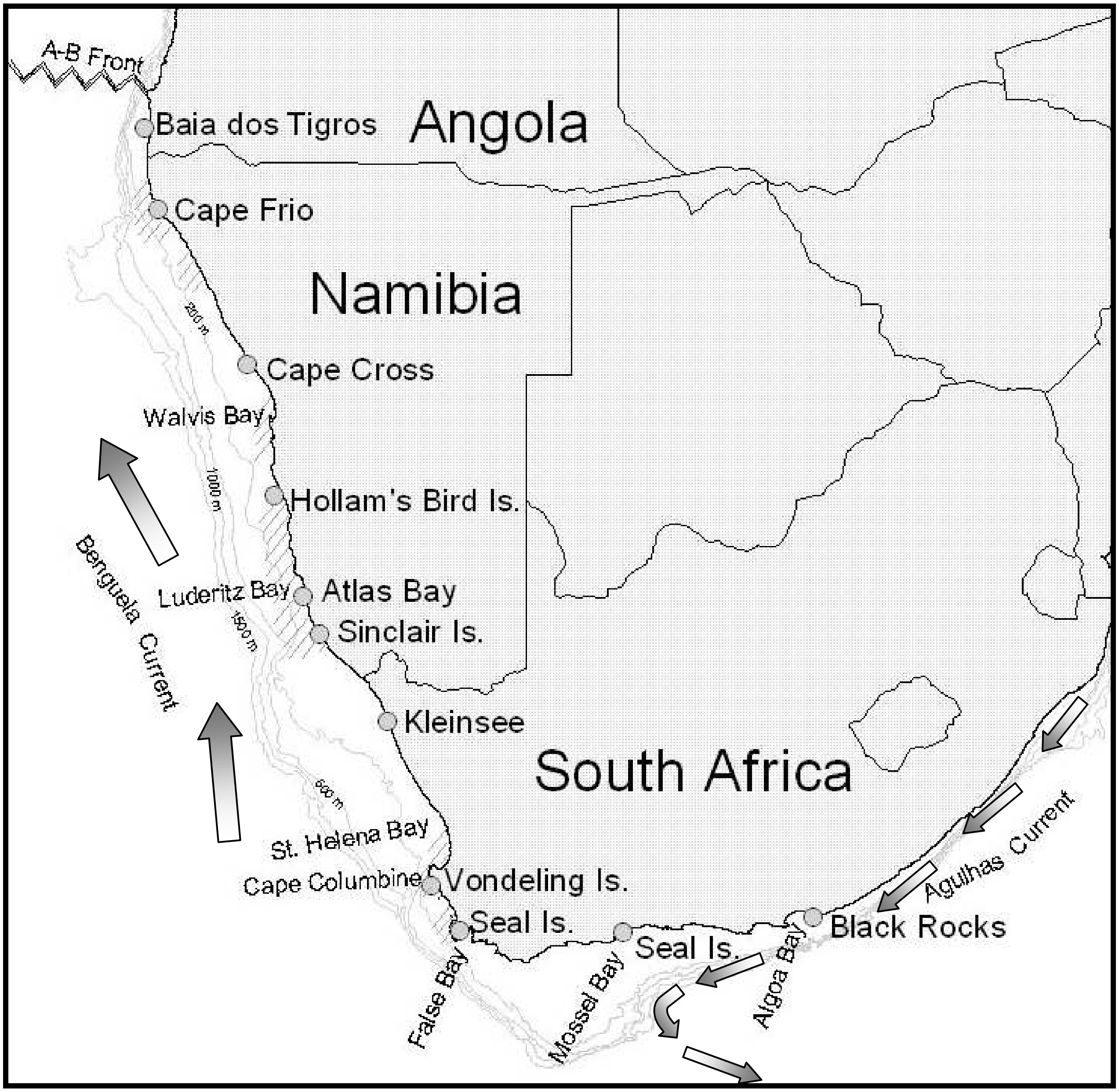

Figure 1 Map of southern Africa showing the locations of selected Cape fur seal breeding colonies (points), the flow directions of the Agulhas and Benguela currents (arrows) and the approximate locations of coastal upwelling cells (diagonal lines) and the Angola-Benguela (A-B) Front.

CHAPTER 2

Making sense of censuses and dealing with missing data: trends in pup counts of Cape fur seal for the period 1971–2003

Abstract

Trends in the population of Cape fur seals *Arctocephalus pusillus pusillus* were estimated from counts of pups on aerial photographs of colonies, taken between 1971 and 2003 to determine trends in the overall population and sub-populations. Incomplete coverage resulted in missing data in some years. Various methods of determining proxy values for missing data were assessed, and it was concluded that different methods were applicable to Namibian and South African colonies. This reflected differences in trends of pup counts between the countries, which were associated with differences in productivity between the southern and northern Benguela Current Ecosystems. In Namibia, temporal changes in pup numbers were non-linear in some years and there was coherence in the temporal patterns between most breeding colonies. This appeared to be on account of an effect of periodic, wide-scale prey shortages that reduced birth rates. There was a northward shift in the distribution of seals in the northern Benguela Current Ecosystem. In South Africa, pup counts were less variable between years, probably on account of a relative stability of food supply. A linear approach was therefore suitable for determining proxy values for missing data at South African colonies. Pup counts suggest that there has been little change in the overall population of the Cape fur seals since 1992, when it was estimated at about 1.7 million animals.

Keywords: abundance, *Arctocephalus pusillus pusillus*, Benguela, distribution, missing data, Namibia, population, South Africa

Introduction

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

The most recent assessment of the Cape fur seal population size, estimated about 1.7 million animals (excluding pups) at the beginning of 1993 (Butterworth *et al.* 1995), indicated that the population had grown about 20-fold during the 20th century. The recovery in numbers followed the imposition of legal controls on sealing at the beginning of the 20th century, and has been perceived as the normal response of a population recovering from overexploitation (Shaughnessy and Butterworth 1981). The recovery was notwithstanding that seals have been unable to re-colonise most of the offshore locations from where they were previously extirpated (Shaughnessy 1984). Instead, new breeding colonies that formed on the mainland during the 20th century have accounted for most of the growth (Rand 1972). It is thought that mainland-based seal breeding colonies were not viable before the arrival of Europeans in southern Africa, owing to the presence of terrestrial mammal predators, including lions *Panthera leo*, brown hyenas *Hyaena brunnea*, black-backed jackals *Canis mesomelas* and also early hunter-gatherers (Shaughnessy and Butterworth 1981). The large mainland colonies have been established in the coastal diamond mining zones of Namibia and South Africa, where terrestrial seal predators had been largely exterminated and human access and disturbance was minimised (Rand 1972).

With the seal population estimated to have doubled in size between 1970 and 1990, it was mooted that the seemingly unlimited breeding space presented by mainland locations, compared with offshore locations, may have caused the seal population size to surpass its pre-sealing level (Griffiths *et al.* 2005). The outcomes of modelling exercises conducted in 1990, around the time when a moratorium was placed on seal harvesting in South Africa, predicted that the seal population would again double within 10 years and treble in 20 years, unless the population was subjected to density dependent effects (e.g. food deprivation) or further sealing (Butterworth and Wickens 1990). Since then, however, sealing has continued off Namibia, where approximately 60 % of the Cape fur seal population occurs (Wickens *et al.* 1991), but not in South Africa. Furthermore, since 1993, there have been at least two mass die offs of seals in Namibia, apparently related to the effects of unfavourable environmental conditions on the distribution and abundance of their prey (Roux 1998, Roux *et al.* 2002). The first of these, in which tens of thousands of seal pups and thousands of adults starved to death in 1994/95 (Roux 1998), was the largest mass die-off recorded for any seal species (Harwood 2002).

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

Censuses of Cape fur seals have been conducted frequently since the early 1970s. The censuses were based on counts of pups on aerial photographs, taken systematically of seal breeding colonies when the numbers of new born pups of the year were expected to be at their maximum. Although these censuses inherently underestimate the numbers of pups in each colony, Shaughnessy (1987) found them to be useful indicators of pup production. However, where trends in pup numbers over time were determined from collective pup counts of colonies, complete aerial coverage in each census year was desirable. Where this was not achieved and counts of one or more colonies were lacking, values need to be inferred for the missing data. Otherwise, censuses of different years are not directly comparable, particularly if one or more of the larger breeding colonies are concerned. Missing data was a recurrent problem in the time-series of Cape fur seal censuses, and the problem has been approached differently between some previous assessments of the population (e.g. Butterworth *et al.* 1987, 1995). However, no attempt has been made to empirically assess the accuracy of alternative approaches for estimating missing data values. In this study, I assessed the accuracy shown by four different methods in approximating the correct values of available counts, with a view to determining the best-suited approach. Once this was achieved and I had inferred missing data values, the trends in pup numbers of the whole population and various sub-populations were investigated, based on all the censuses that have been completed to date (1971–2003). The pup count trends were interpreted and the relationship between recent trends (especially since 1992) and the status of the seal population (all age-classes inclusive) was discussed.

Material and Methods

Background

The procedure for censusing the Cape fur seal pup population using aerial photography is given in detail in Annex 1 of this thesis. Briefly, near vertical, serial overlapping photographs were taken from aircraft flying parallel flight paths over colonies at a height of c. 100 m. For large colonies, high altitude pictures (c. 300 m) of the colony were also taken, to assist with fitting of the lower altitude prints to map the colony. The timing of photographing were standardised, taking place during 16–22 December each census year, except where otherwise indicated (see Appendix 1).

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

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[1] In 1971, a single counter was used, and in 1976, the geometric mean rather than the arithmetic mean was used

In this study, I referred to each census by the year in which it occurred, i.e., 2003 refers to the census that was conducted in December 2003. Between 1970 and 2003, a census was conducted in all but five years, with the number of colonies that were surveyed varying between census years (see Appendix 1). Seal colonies were also photographed in 2004, 2005 and 2006, but the pup counts were as of yet incomplete and therefore unavailable for this study.

Breeding and non-breeding colonies

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

Accounting for missing data in censuses

Since 1990, assessments of the size and trend of the pup population (e.g. Butterworth and Wickens 1990, Wickens *et al.* 1991, Butterworth *et al.* 1995) made use only of data from the census years in which comprehensive coverage of the pup population was attained. Such years were referred to here as “full census” years, which I defined as a year in which two-thirds of the number of recognised breeding colonies were successfully covered. Following this criterion, there were 13 full census years between 1970 and 2003. Although census coverage in 2003 was slightly below two-thirds (65 %), it was included on the grounds that the four largest colonies (Kleinsee, Cape Cross, Atlas Bay and Wolf Bay) where, on average, some two thirds of all pups are born, were all successfully censused in this year. The remaining census years, in which counts of one or more colonies were conducted but no attempt was made to cover all or most of the population, were referred to as “partial census” years.

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[2] Reports (e.g. MAM, Department of Environmental Affairs, pers. comm.) of increased numbers of pups born at locations not listed in the Appendix, where breeding was non-existent or sporadic during the period of this study, e.g. Vondeling Island (33°09’ , 17°58’), Robberg (34°06’, 23°24’), North Reef (27 °00’, 15°19’) and Sylvia Hill (25°08’, 14°51’), will only be verified once the counts of more recent censuses (2004-2006) are complete

Complete census coverage is desirable to determine the size and trend of the whole pup population. However, even in most full census years, counts from one or more breeding colonies were either lacking or were inadequate and could not be used (referred hereafter to as "missing counts"). Reasons for this included (a) omission of a colony during a census (e.g. for logistical reasons or owing to weather conditions), (b) incomplete coverage of one or more colonies, (c) poor-quality photographs of one or more colonies (e.g. owing to fog, photographing from too high an altitude, equipment failure or exposure of film) and (d) human disturbance to a colony prior to censusing (Shaughnessy 1987, Butterworth and Wickens 1990). For censuses to be comparable, proxy values for missing counts need to be determined. In some past studies, such values have been inferred either by using the next or previous count for the same colony or linear interpolation between the two (e.g. Wickens *et al.* 1991, Butterworth *et al.* 1995). However, considering that the pup counts at certain colonies showed considerable between-year fluctuations especially during the latter half of the time-series (see Appendix 1), proxy values inferred using the above methods would be highly inaccurate in many cases. Bearing in mind that approximately two-thirds of all pups are produced at four large mainland colonies, unrealistic proxy values for these colonies could significantly influence estimates of the size and trend of the pup population or subsets of the pup population.

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

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

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

Method 1 – nearest count

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

Method 2 – Linear interpolation

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

$$x_j = X_{jp} + \frac{X_{jn} - X_{jp}}{j_n - j_p} * \left(j - j_p\right) \tag{2}$$

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

Method 3 – weighted mean

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

$$\bar{x}\left(w_j\right) = \frac{\sum_{j=1}^{J}\left(X_j * w_j\right)}{\sum\left(w_j\right)} \tag{3}$$

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

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

Method 4 – Iterative imputing

Proxy values for SMVs were determined with the approach for imputing missing observations used for indices of waterbird populations in Britain (Prŷs-Jones *et al.* 1994). This method utilises an algorithm developed by Underhill and Prŷs-Jones (1994) for imputing proxy values. The algorithm was based on the view that, apart from random deviation, each proxy value can be modelled as a product of two factors, in this case a colony factor and a year factor. Simply, the procedure takes the trends in the pup counts at other colonies into account in determining proxy values. In the case of waterbird populations in Britain, Underhill and Prŷs-Jones (1994) assumed that a single model could be applied to the whole of Britain, and did not impute proxy values for missing data regionally. However, trends in abundance of Cape fur seal pups in southern Africa vary between colonies (Shaughnessy 1987, Butterworth and Wickens 1990), and it would be inappropriate, for example, if counts of Black Rocks (Algoa Bay) were to influence imputed values at Cape Cross, considering the differences in their location and size.

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

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

(1) Each group of associated colonies was arranged in a matrix of colony by full census year (i.e. partial census years were excluded from the matrix);

(2) Each cell in the matrix that had missing data (including the relevant SMV) was replaced with an initial estimate of the missing value (the final estimate of the imputed value was not dependent on this choice). Following Underhill and Prŷs-Jones (1994), the mean of all existing counts (including from full and partial census years) were used for each colony as the initial estimate;

(3) The sum of each row and each column were calculated;

(4) The initial estimates of missing values with new values were replaced using the updating formula

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

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

(5) Steps 3 and 4 were repeated until the changes between successive iterations became minimal;

(6) At each iteration: if χ_{ij} of a cell that previously contained an undercount (i.e. cells flagged a–e in Appendix 1) was lower than the original undercount, it was replaced by the original undercount. This was based on the rationale that, because numbers tend to be underestimated by counts, a known undercount was likely to be nearer the true number than an even lower imputed value (Underhill and Prŷs-Jones 1994).

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

Analysis of trends in the pup population

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

To standardise the comparisons, only the full census years were used, for the population as a whole and the various subpopulations. Trends in pup counts were assessed for the period between the first and the most recent available full censuses (1971–2003) and for two periods within the time-series, namely 1971–1992 and 1992–2003.These two time periods were chosen because (a) there were equal numbers of full censuses in each time period ($n = 7$), (b) in Namibia, where approximately 60 % of the Cape fur seal’s pup production occurs in most years (this study), trends in pup numbers before and after 1992 show a major discontinuity (van der Lingen *et al.* 2006), and (c) the most recent published assessment of the size and trend of the seal population (Butterworth *et al.* 1995) included records up to 1992.

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

$$r = e^{b} \tag{5}$$

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

$$r = (r - 1) * 100 \tag{6}$$

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

Results

Comparison of methods for determining missing data

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

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

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

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

Method 4 was used to impute the proxy values for the missing counts of the two groups of Namibian colonies distinguished in Figure 2. In the group comprising Atlas Bay, Wolf Bay, van Reenen Bay and Long Islands, Method 4 had produced relatively accurate proxy values for SMVs at the first three colonies, but highly inaccurate values for the last colony (Table 1). In this case, the method was affected by there being many empty cells in the matrix of colony by full census year among the first three colonies in the group (including five for each of Wolf Bay and Atlas Bay), and one year (1976) in which there were no reliable counts for any of these three colonies. However, because there were no missing counts for Long Islands in full census years, and thus no need to impute proxy values for this colony, I adhered to this grouping.

Trends in the pup population

Pup count totals for the whole population and subsets of the population, with missing data imputed by proxy values, are plotted against time in Figure 3. Between 1971 and 1992, pup counts of the whole population (3.1 % per year), Namibia (3.3 %) and South Africa (2.8 %) increased significantly (Table 3). However, most growth over this period occurred at the mainland colonies of both countries (Namibia mainland = 4.3 %; South Africa mainland = 4.1 %), and in areas with mainland colonies (Area 1 = 6.9 %; Area 2 = 2.8 %; Area 3 = 2.8 %). Pup counts at offshore colonies generally fluctuated between the period 1971 and 1992, and no significant change in numbers could be detected for that period.

The period 1992–2003 was characterised by considerable fluctuations in pup counts (Figure 3), particularly in Namibia, which would have reduced the ability of the analysis to detect significant changes (Table 4). In most cases, the confidence intervals about the estimated percentage annual rate of change were broad. In South Africa, the rate of increase in pup counts over this period (1.6 %) bordered on significance, as did the rate of increase for area 4 (4.7 %).

Over the entire time-series (1971–2003), the rates of increase for South Africa (1.7 %), mainland and offshore colonies in South Africa (2.1 % and 1.5 % respectively), and area 1 (4.2 %), area 3 (1.5 %) and area 5 (2.1 %), were all significant (Table 5). The rate of increase for the whole pup population (1.2 %), and the rate of decline in area 6 (-2.5 %), both bordered on significance.

Discussion

Pup counts as indicators of annual pup production

Two methods have been employed in the past to estimate the numbers and trends of Cape fur seal pups, namely counts of pups on aerial photographs, and pup population size estimates from tag-recapture experiments (Shaughnessy 1987, 1993). Aerial photographic censuses of pups are the most practical means of assessing the population owing to the large number and wide geographical distribution of the colonies. Therefore, they comprise the longest and most complete time-series of pup numbers, from 1970 to the present, and have formed the basis of most assessments of the seal population's size or trend (e.g. Wickens *et al.* 1991, Butterworth *et al.* 1995). Although tag-recapture operations were considered by Shaughnessy (1993) to be the more accurate method, they are time-consuming and costly, and require a lot of manpower. Therefore, they could only be applied in a few colonies during any given year, and they were discontinued in Namibia and South Africa in 1989 and 2002 respectively (Department of Environmental Affairs, unpubl. data).

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

Although different counters were used during the time-series, one person (MAM) oversaw the process throughout, and supervised the training of new counters. I have therefore assumed that counting over the course of the time-series has been fairly consistent. However, improvements in the quality of photographs, owing to improvements in censusing equipment and methods, would have resulted in greater accuracy of counts, and would likely increase estimates of the rates of change in pup numbers over time. Butterworth *et al.* (1995) found that a switch from flying with a fixed-wing aircraft to a helicopter, when censusing most of the South African colonies, did not seriously compromise the compatibility of counts. More recently, there has been a switch from black and white film to colour digital photography. This occurred in 2005 and therefore does not affect the present study (up to 2003). For future assessments, the effects of using different photographic technology must be taken into consideration in seal counts.

Accounting for gaps in the pup count time-series

Where pup counts of colonies were used collectively to determine rates of change for the whole pup population or subsets of it, it was necessary to determine values for counts of colonies that were missing in any years. In Butterworth *et al.* (1987) and Butterworth and Wickens (1990), missing counts at colonies were estimated from separate linear models of the log-transformed counts available for each colony. In this way, values for each colony were estimated for every year in the time-series, and pup numbers for the whole population in each year were calculated by summing the values for all the colonies. This approach was rejected after it became apparent that fluctuations in pup counts between years resulted in poor fits of the models to the available count data of many colonies (Butterworth and Wickens 1990). A simpler method was subsequently adopted (Wickens *et al.* 1991, Butterworth *et al.* 1995), whereby only the years with comprehensive censuses (full census years) were used to model the pup census values of the population as a whole. The same approach was used to determine pup numbers and trends in this study. This still requires that inferences be made for gaps in the data in full census years, because using only the totals of the available counts could give a misleading impression of the population trend, particularly when counts for large colonies were missing in a year. In the aforementioned studies, gaps in the count data were filled using linear interpolation between the previous and the next counts of the same colony, or by inferring the same value as a neighbouring count in the time-series for the same colony. Inspection of the time-series (see Appendix 1) shows that neither approach was always satisfactory. For example, estimating proxy values in place of the existing 1997 counts at Wolf Bay and Atlas Bay from the 1995 and 2001 counts of these colonies, respectively, results in underestimates of the existing counts by about 70 %. It follows that either approach would have caused the 1997 pup count for the Namibian seal population, and for the whole seal population, to be underestimated by about 30 % and 20 % respectively.

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

Causes of these general differences in the pup count trends of colonies between the two countries are discussed later.

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

The 1971 census was the first full census, and was therefore the “anchor” year of the time-series. This census has been acknowledged to be less reliable than subsequent full censuses, because certain errors have become apparent (Shaughnessy 1987). Most significantly, the number of pups harvested at the Wolf Bay and Atlas Bay colonies (c. 42 200 for the two colonies combined) was substantially higher than the pup counts at these colonies (c. 16 300), probably on account of incomplete aerial coverage (Shaughnessy 1987). Wickens *et al.* (1991) and Butterworth *et al.* (1995) replaced the original counts with the next available reliable counts in the time-series for these two colonies. Given the harvest returns, this proxy value (c. 54 300 for the two colonies combined) was considered by Wickens *et al.* (1991) not to be unrealistic, assuming a low mortality rate between the census and harvesting in that year. This value was similar to the value of c. 53 700 imputed in this study for Wolf Bay and Atlas Bay combined. As these were the only large colonies for which it was necessary to determine proxy values for 1971 in this study, the total pup count estimate for this year (all colonies) was similar to the value estimated in previous studies (e.g. Wickens *et al*. 1991)

The 1985 full census has been omitted from some previous assessments of the seal population (e.g. Wickens and Butterworth 1990, Wickens *et al.* 1991), on the grounds that male harvesting, which was allowed in Kleinsee, Atlas Bay and Wolf Bay at the time, extended well into the pupping season and caused disturbance. Consequently, the low counts for these colonies (see Appendix 1) were considered to be non-representative of the numbers born there in 1985. Here, I determined proxy values for these three colonies for 1985 (Table 2), which in the case of the two Namibian colonies were each lower than the existing counts of the preceding and succeeding censuses (Appendix 1). Correspondingly, the total pup counts for Namibia and for the whole population were relatively low (Figure 3a). I considered this to be realistic, given that environmental conditions in the northern Benguela Current Ecosystem in 1984–1985 were known to have decreased the productivity of the system and depleted the stock sizes of several of the seals' prey species (Roux 2003), and may therefore have impacted on the birth rate of the seal population (discussed later).

Interpreting the trends in pup numbers

Censuses of pup numbers have frequently been used as indicators of the overall size of seal populations, assuming some fixed ratio between pup numbers and older age-classes in the population (e.g. Pistorius *et al.* 1999, Kirkwood *et al.* 2005). A factor of 4.0 (David 1987), later revised to 4.8 after more accurate information became available (Butterworth *et al.* 1988), have been employed to estimate the size of the Cape fur seal population size from pup census results. However, Wickens and Shelton (1992) showed that trends between pup numbers and the seal population size can differ as a result of variability in life history parameters (e.g. survival rates, pregnancy rates) and harvesting of pups and males. Thus, caution needs to be used in inferring seal population numbers and trends directly from pup counts. The considerable fluctuations in pup counts that occurred between 1992 and 2003, particularly in Namibia, are a case in point (Figure 3a). The reduced pup counts in the census years between 1992 and 1997, and again between 1997 and 2003, were associated with unfavourable environmental/feeding conditions in the northern Benguela Current Ecosystem during 1994–1995 and again in 2000–2001, which caused the starvation and deaths of tens of thousands of seals (pups and older animals) in Namibia (Roux 1998, Roux *et al.* 2002). Prey shortages also impact negatively upon birth rates of seals (Guinet *et al.* 1998), and the years of unfavourable feeding conditions were marked by a high incidence of abortions at many Namibian colonies during winter (Roux 1998, 2002). Given that pup counts had recovered rapidly by the time of the 1997 and 2003 censuses, to numbers comparable to the census before each downward flux, it is probable that reduced birth rates of adult females (e.g. because of failure to come into oestrus, failure to implant or failed pregnancies) rather than adult female mortality, were mainly responsible for the reduced pup counts in Namibia in 1994–1996 and 2001. Multiplying the number of pup births by a constant factor to estimate the numbers of seals in older age-classes would have resulted in a considerable underestimation of the Namibian and overall seal population sizes in years affected by low birth rates.

A better method of assessing the size of the seal population, than simply inferring it annually from pup counts, is to model the population based on demographic parameters and long-term trends in pup numbers (Wickens and Shelton 1992). Butterworth *et al.* (1995) estimated the seal population (South Africa and Namibia) for 1992 at about 1.7 million individuals (excluding pups). In the present study, the considerable variability in pup counts between years, together with the shortness of the time-series, reduces the ability of the statistical analysis to detect significant changes in pup numbers during 1992–2003. This applies to the whole population and some of the sub-populations defined in this study (particularly in Namibia). However, if it is assumed that the birth rates of the whole population in 1992, 1997 and 2003 (the only three census years in the latter time period with comparatively high pup counts) were similar, it appears that the seal population has stabilised at around its 1992 level, based on the pup counts (Figure 3a). This is contrary to the prediction that the seal population would double between 1989 and 1999, assuming conditions of no further harvesting after 1989, and an absence of density dependent effects on the population (Butterworth and Wickens 1990). Effects of continued harvesting in Namibia may have contributed to the decline in the growth rate of the population. However, circumstances (discussed below) support the view that the main cause of the reduced rate of increase during 1992–2003 compared with 1971–1992 (Tables 3 and 4) was the effect of reduced prey availability on the carrying capacity of the population.

The environmental perturbations that occurred in the northern Benguela Current Ecosystem between 1992 and 1994 caused large declines of fish stocks as a result of death, dispersal and poor recruitment. These events included an extended low-oxygen event affecting shelf waters off Namibia, and a severe Benguela Niño event that caused a warm-water intrusion onto the Namibian shelf (Gammelsrød *et al.* 1998). It was believed that continued high levels of fishing during these unfavourable periods exacerbated the effects on some fish stocks (Boyer and Hampton 2001). The biomass levels of marine biota (including prey species of seals) in the northern Benguela Current Ecosystem have not yet recovered to their previous levels (Cury and Shannon 2004), despite reduced fishing pressure there since 2000 (van der Lingen *et al.* 2006). This was interpreted as an indication of a “regime shift” in the ecosystem, and it was considered unlikely that a recovery will occur within a short time period (Cury and Shannon 2004). The productivity of other top predators besides seals in the northern Benguela Current Ecosystem also appeared to have been affected by the reduced availability of prey. These include seabirds such as the African penguin *Spheniscus demersus* and Cape gannet *Morus capensis* (Crawford *et al.* 1995, Kemper 2006).

In Namibia, it was noteworthy that, whereas area 2 accounted for 62 % of Namibia's pup numbers in 1992, it accounted for 56 % and 50 % in 1997 and 2003 respectively. Correspondingly, area 1 accounted for 28 %, 30 % and 37 % of Namibia's pups. The pup counts in area 3 (which also includes Kleinsee in South Africa) increased by 22 % from 1992 to 1997. Given the rapid rate of growth in pup numbers at Cape Frio (Figure 1) in area 1, dispersal of adults appears to have played an important role in the changing distribution of the population in Namibia. Cape Frio was described as a non-breeding colony by Oosthuizen and David (1988); pup counts between 1992 and 2003 increased at about 30 % per annum (95 % CI 11–52 %, $F_{1,5} = 19.13$, $p < 0.05$; see Appendix 1). This rate could only have been sustained by immigration, because the maximum intrinsic rate of increase of a fur seal colony is about 17 % per annum (Payne 2002).

The distributional shifts in the seal population in Namibia were likely in response to shifts in the geographical distribution of prey (van der Lingen *et al.* 2006). This was supported by the fact that the decline in area 2 was not confined to the mainland sites of Wolf Bay and Atlas Bay, as would be expected if effects of harvesting were driving the changes, but was also evident at offshore locations. Harvesting activity in area 2 was restricted to these two mainland sites throughout 1992–2003; at these sites pup counts in 1997 and 2003 were 81 % and 73 % of their 1992 level respectively. The corresponding counts at offshore colonies in area 2, where no harvesting took place, were 71 % and 65 % of their 1992 level, suggesting a common cause for the declines on both the mainland and the islands – probably prey availability.

Previously, in 1984, another severe Benguela Niño event that severely affected fish stocks occurred in the northern Benguela Current Ecosystem (Roux 2003). No census coincided with the occurrence of the event, but the relatively low pup count for Namibia (and the whole population) in 1985 may reflect a reduced birth rate influenced by this event. The breeding populations of Cape gannets, Africa penguins and bank cormorants *Phalacrocorax neglectus* in Namibia were also reduced at this time, compared with preceding and succeeding censuses (Crawford *et al.* 1995, 1999, van der Lingen *et al.* 2006).

The seal population has been considerably more stable off South Africa than off Namibia between 1971 and 2003. This suggests that the southern Benguela Current Ecosystem has not been subjected to environmental perturbations of the same strength or effect as the northern Benguela Current Ecosystem over that period. Also, fish stocks appear to have benefited from relatively conservative fisheries management strategies implemented by South Africa over the past several decades (Cury and Shannon 2004). Nevertheless, there have been recent shifts in the geographical distribution of important pelagic prey species in the southern Benguela Current Ecosystem, most importantly, the eastward shift in the distribution of the sardine *Sardinops sagax* stock since 2001 (van der Lingen *et al.* 2005, 2006). However, whereas changes in the geographical distribution and abundance of prey in the northern Benguela Current Ecosystem have apparently influenced large-scale distributional shifts in Namibia's seal breeding population (see above), there is less scope for the breeding population to track the spatial shifts in prey availability taking place in the southern Benguela Current Ecosystem. South of Kleinsee (Figure 1), the colony where the bulk of South Africa's seal population breeds, nearly all the recognised seal breeding colonies occur on small offshore locations (≤ 2.8 ha, Rand 1972), offering little or no space for further growth of existing colonies. Up to now, seal colonies have been prevented from re-establishing at most of the larger islands off South Africa from where seals were previously eradicated (Shaughnessy 1984). Moreover, there is little scope for breeding colonies to establish themselves on the mainland along the south-west or south coasts of South Africa (Areas 4–6), because the potential for human interference is greater than in the largely restricted or reserved coastlines of Namibia and the Northern Cape province (Stewardson 1999). Therefore, the combination of limited breeding space and spatial shifts in the availability of prey in the southern Benguela Current Ecosystem may have contributed to the perceived stabilization in growth of South Africa's seal population in 1992–2003 compared with 1971–1992 (Tables 3 and 4).

Nevertheless, pup counts for the offshore colonies in South Africa, and for area 5 which consists of offshore colonies, increased significantly from 1971 to 2003 (Table 5). The establishment and growth of breeding colonies at Paternoster Rocks and Bird Island in Lambert's Bay (Figure 1) since the late 1980s, explains some of the perceived growth at offshore colonies, though not for area 5. Early in the census time-series, Shaughnessy (1987) described the Quoin Rock and Elephant Rock colonies as being well below their carrying capacities as a result of over-harvesting of pups. Pup harvesting figures reported by Wickens *et al.* (1991) show a similar situation for Geyser Rock and Seal Island (Mossel Bay). After adjusting the pup counts in

Appendix 1 upwards to compensate for undercounting[3] and pup mortality[4], it was calculated that harvest rates at these two colonies were on occasions as high as 63 % (1971) and 100 % (1974) respectively of the pups born there. This was despite the fact that the harvesting rate recommended for a maximum sustainable yield was estimated to be between 30 % and 35 % of the pup numbers available (Shaughnessy and Best 1982). Therefore, with the cessation of pup harvesting at the island colonies in the late 1970s and early 1980s, the higher pup counts in subsequent censuses, at least at the above four locations (see Appendix 1), probably resulted from compensatory growth. This would have had a positive effect on the trends in pup counts over the entire times-series.

In summary, numbers increased significantly from 1971 to 1992, both in Namibia and South Africa, with mainland colonies accountable for most of the growth. Significant changes could not be detected for the period 1992–2003, owing to considerable year-to-year variability between pup counts, especially in Namibia. There was a northward shift in the distribution of seals in the northern Benguela Current Ecosystem. Based on the pup counts in years that were apparently "favourable" for pup production, there appears to have been little change in the overall population size since 1992, when it was estimated at about 1.7 million animals.

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[3] A factor of 1.05, estimated to scale pup counts to tag-recapture estimates of pup numbers at island colonies (Butterworth and Wickens 1990)

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

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

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

Table 2 The proxy values for missing pup counts of Cape fur seal colonies (indicated by blocked cells in Appendix 1) in South Africa and Namibia, determined using either Methods 2 or Method 4 (see text for details).

Year	Colony	Proxy value	Year	Colony	Proxy value
1971	Wolf Bay	20 607	1994	Boat Bay Rock	702
	Atlas Bay	33 092		Dumfudgeon Rock	785
	Black Rock	380		Seal Is, Mossel Bay	872
	Seal Is, False Bay	12 520		Black Rocks, Algoa Bay	380
1976	Wolf Bay	17 423	1995	Marshall Reef	307
	Atlas Bay	27 979		Staple Rock	1 280
	van Reenen Bay	3 240		Boat Bay Rock	779
1979	Marshall Reef	473		Dumfudgeon Rock	871
	Hollamsbird Is	3 308		Seal Is, Mossel Bay	930
	Wolf Bay	21 102		Black Rocks, Algoa Bay	338
	Atlas Bay	33 888	1996	Dumfudgeon Rock	891
	Lions Head	2 431		Wolf Bay	21 427
	Jacobs Reef	3 452		Atlas Bay	34 410
1982	Marshall Reef	446	2001	Jacobs Reef	2 801
	Staple Rock	1 859		Robbesteen	990
	Kleinsee	77 393		Geyser Rock	11 184
1985	Hollamsbird Is	2 917	2003	Marshall Reef	434
	Wolf Bay	23 485		Staple Rock	1 808
	Atlas Bay	37 714		Boat Bay Rock	1 100
	Albatross Rock	2 811		Dumfudgeon Rock	1 230
	Kleinsee	79 929		Albatross Rock	2 926
	Seal Is, Mossel Bay	1 102		van Reenen Bay	5 121
	Black Rocks, Algoa Bay	746		Geyser Rock	11 184
1988	Seal Is, Mossel Bay	1 215		Quoin Rock	1 223
1993	Marshall Reef	277		Seal Is, Mossel Bay	658
	Staple Rock	1 154			

Table 3 Results of linear regressions between the natural logarithms of Cape fur seal pup counts and years (1971–1992). The percentage change in pup counts per year (% r) is given with 95 % confidence intervals in parentheses. Also shown is the F statistic of the ANOVA testing whether the slope of the linear regression was significantly non-zero.

Population part	Regression	R^2	$F_{1,5}$	P	% r	95 % CI
Whole population	y = 0.030x - 47.888	0.86	31.80	**<0.05**	3.08	(1.67 – 4.52)
Namibia	y = 0.032x - 51.759	0.73	13.33	**<0.05**	3.26	(0.95 – 5.62)
SA	y = 0.027x - 42.875	0.79	18.75	**<0.05**	2.78	(1.12 – 4.46)
Namibia offshore	y = 0.007x - 2.770	0.06	0.31	0.60	0.68	(-2.40 – 3.84)
Namibia mainland	y = 0.042x - 70.980	0.82	22.24	**<0.05**	4.25	(1.91 – 6.64)
SA offshore	y = 0.010x - 10.344	0.11	0.64	0.46	1.05	(-2.290 – 4.50)
SA mainland	y = 0.040x - 68.006	0.70	11.55	**<0.05**	4.07	(0.98 – 7.25)
Area 1	y = 0.067x - 122.800	0.83	24.59	**<0.05**	6.94	(3.29 – 10.73)
Area 2	y = 0.026x - 43.089	0.60	7.43	**<0.05**	2.79	(0.16 – 5.50)
Area 3	y = 0.028x - 43.413	0.79	18.39	**<0.05**	2.80	(1.11 – 4.51)
Area 4	y = -0.014x + 37.406	0.16	0.97	0.37	-1.43	(-5.07 – 2.35)
Area 5	y = 0.023x - 37.000	0.43	3.75	0.11	2.40	(-0.77 – 5.67)
Area 6	y = -0.032x + 70.331	0.16	0.97	0.37	-3.12	(-10.81 – 5.23)

Table 4 Results of linear regressions between the natural logarithms of Cape fur seal pup counts and years (1992–2003). The percentage change in pup counts per year (% r) is given with 95 % confidence intervals in parentheses. Also shown is the F statistic of the ANOVA testing whether the slope of the linear regression was significantly non-zero.

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

Table 5 Results of linear regressions between the natural logarithms of Cape fur seal pup counts and years (1971–2003). The percentage change in pup counts per year (% r) is given with upper and lower 95 % confidence intervals in parentheses. Also shown is the F statistic of the ANOVA testing whether the slope of the linear regression was significantly non-zero.

Population part	Regression	R^2	$F_{1,11}$	P	% r	95 % CI
Whole population	y = 0.015x - 10.457	0.27	4.02	0.07	1.16	(-0.11 – 2.44)
Namibia	y = 0.007x - 2.145	0.06	0.65	0.44	0.70	(-1.21 – 2.66)
SA	y = 0.017x - 22.410	0.73	29.02	**<0.05**	1.72	(1.01 – 2.43)
Namibia offshore	y = -0.013x + 35.700	0.21	2.96	0.11	-1.26	(-2.86 – 0.36)
Namibia mainland	y = 0.014x - 15.980	0.17	2.19	0.17	1.39	(-0.67 – 3.50)
SA offshore	y = 0.014x - 18.286	0.42	8.05	**<0.05**	1.45	(0.32 – 2.60)
SA mainland	y = 0.020x - 29.221	0.52	12.09	**<0.05**	2.05	(0.75 – 3.36)
Area 1	y = 0.041x - 70.766	0.72	28.81	**<0.05**	4.17	(2.44 – 5.93)
Area 2	y = -0.007x + 25.263	0.03	0.34	0.57	-0.70	(-3.31 – 1.98)
Area 3	y = 0.015x - 18.414	0.54	13.16	**<0.05**	1.51	(0.59 – 2.43)
Area 4	y = 0.007x - 5.854	0.08	0.97	0.35	0.75	(-0.91 – 2.43)
Area 5	y = 0.020x - 30.426	0.59	15.82	**<0.05**	2.06	(0.91 – 3.21)
Area 6	y = -0.025x + 57.685	0.30	4.76	0.05	-2.50	(-4.97 – 0.02)

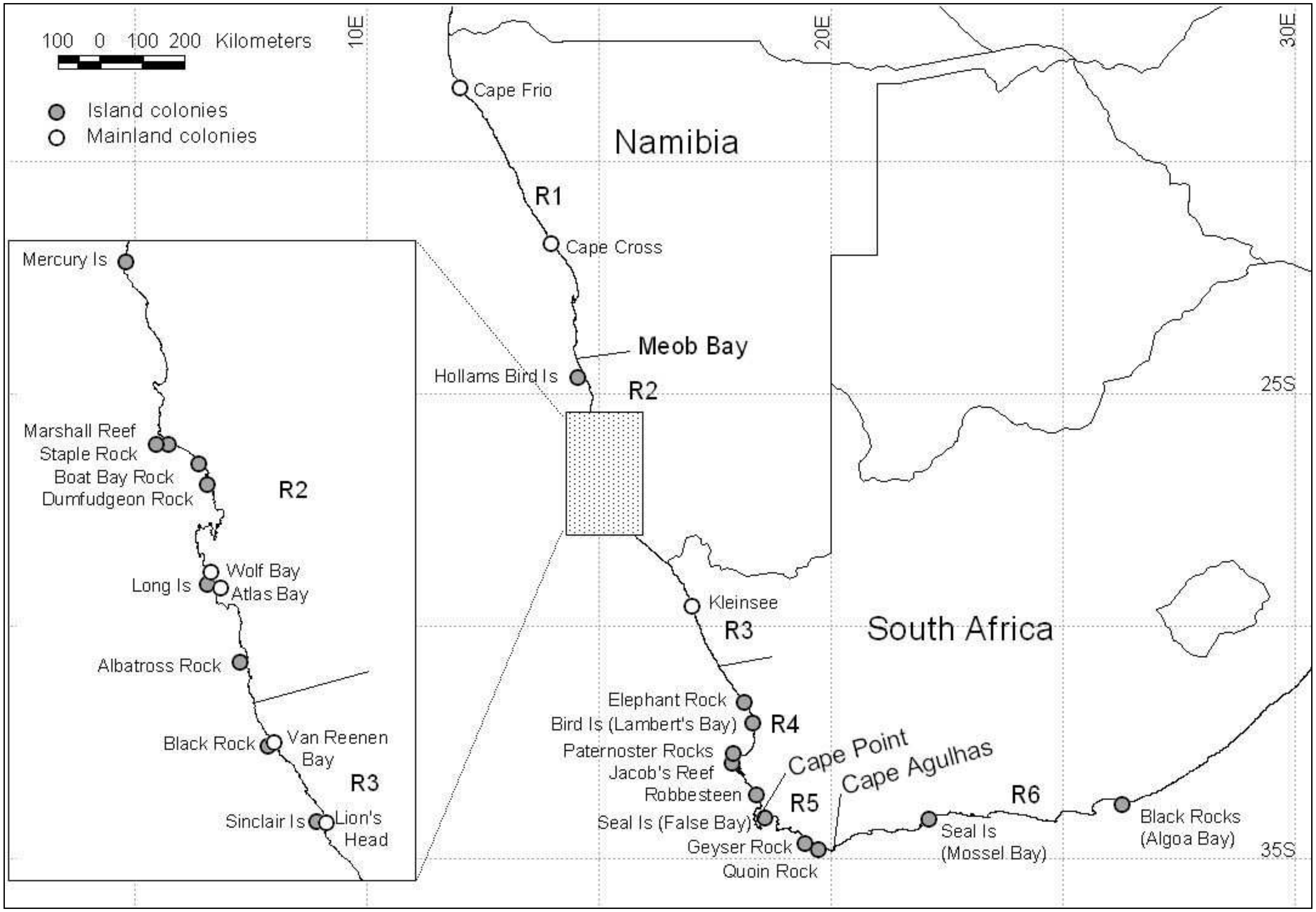

Figure 1 Distribution of Cape fur seal population in South Africa and Namibia, showing mainland and island breeding colonies. Areas 1–6 are indicated as A1–A6, and separated by straight lines drawn inland from the coast.

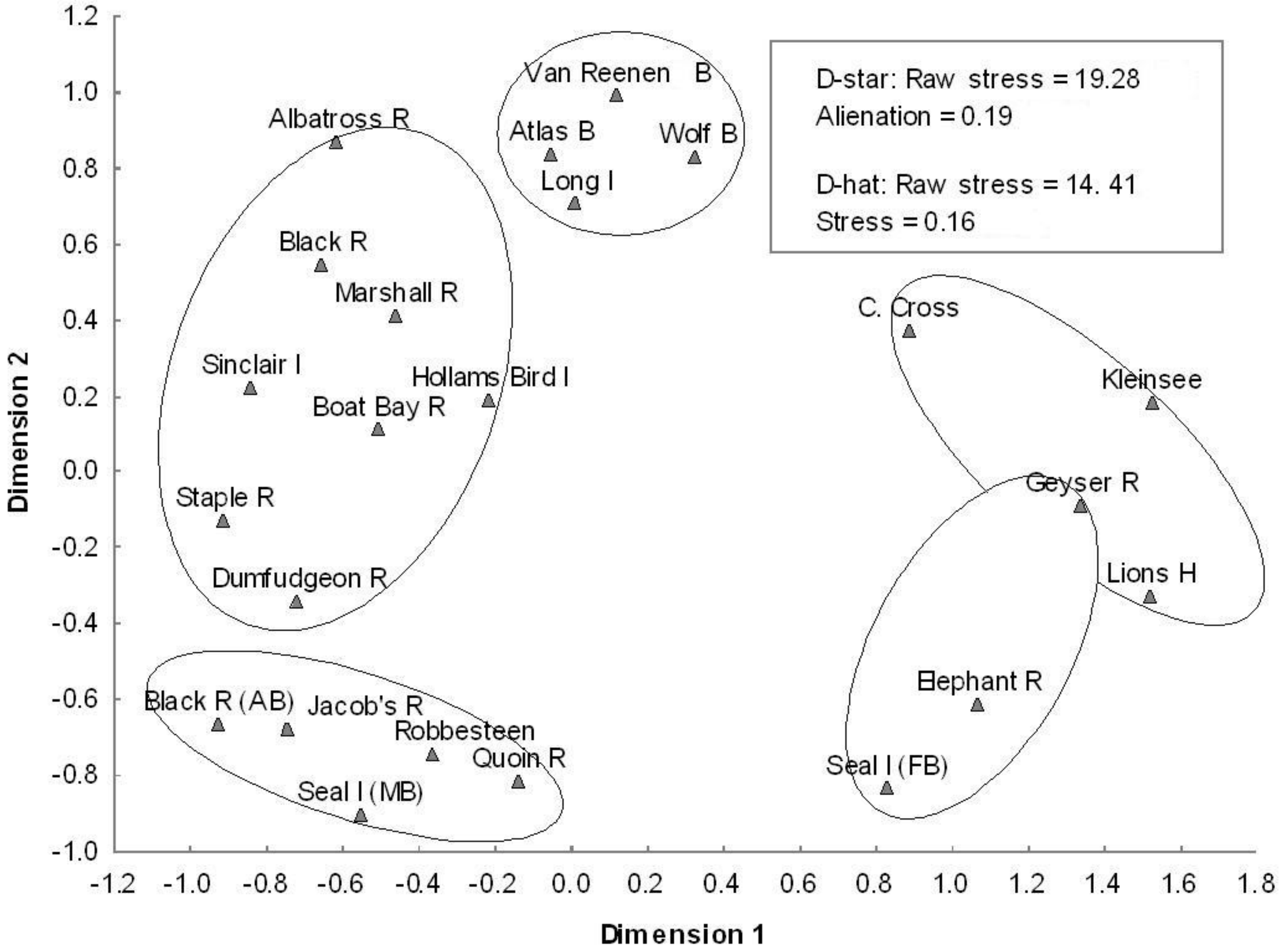

Figure 2 Two-dimensional scatter-plot produced by Nonmetric Multidimensional Scaling for the relationships between trends in counts of Cape fur seal pups at colonies in South Africa and Namibia.

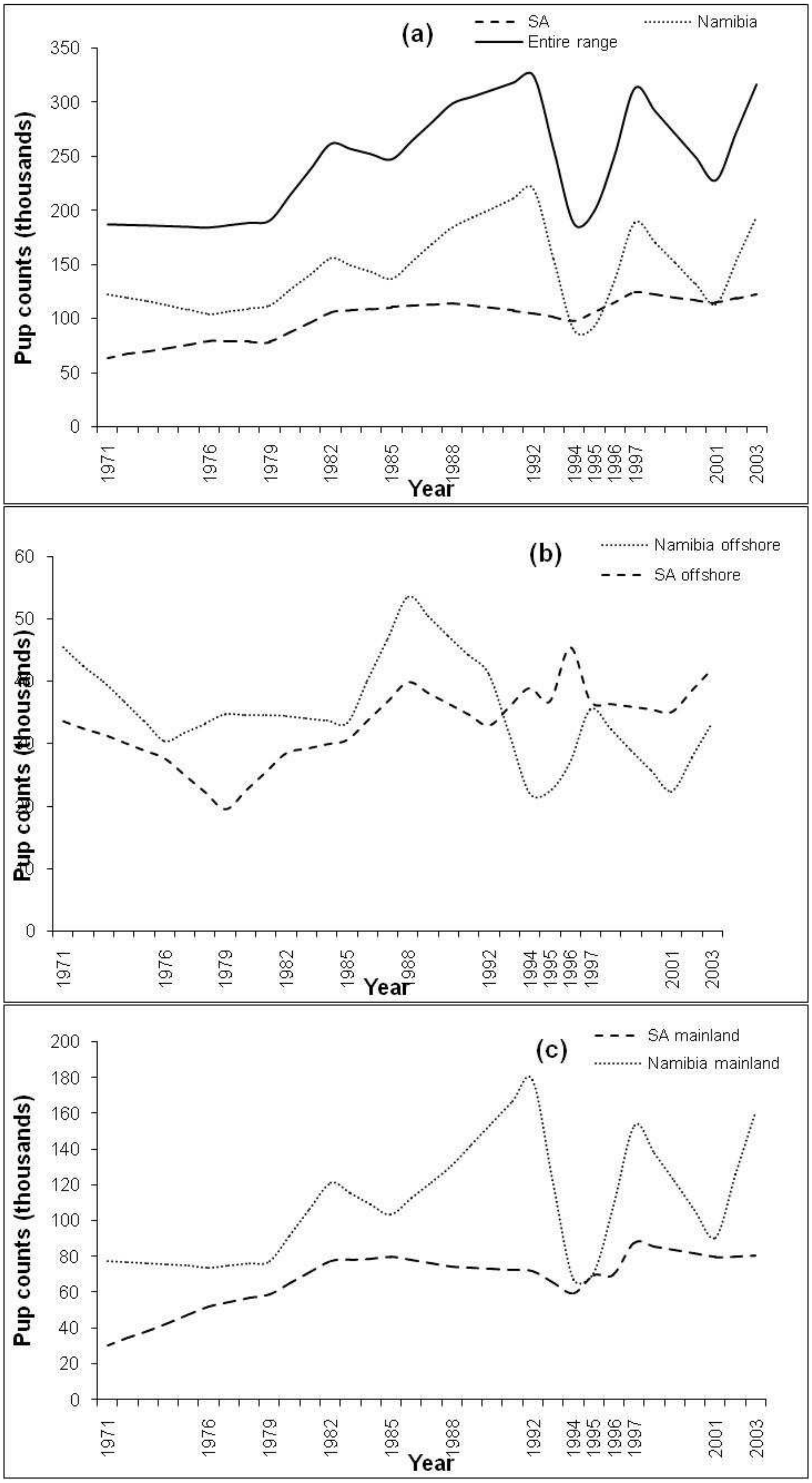

Figure 3 Trends in pup counts of Cape fur seals in South Africa and Namibia between 1971 and 2003, based on aerial photographs by (a) country, (b and c) colony type (offshore or mainland) within each country and (d–f) area (A1–A6). Only counts from full census years are presented. Note the differences in scale between the y-axes.

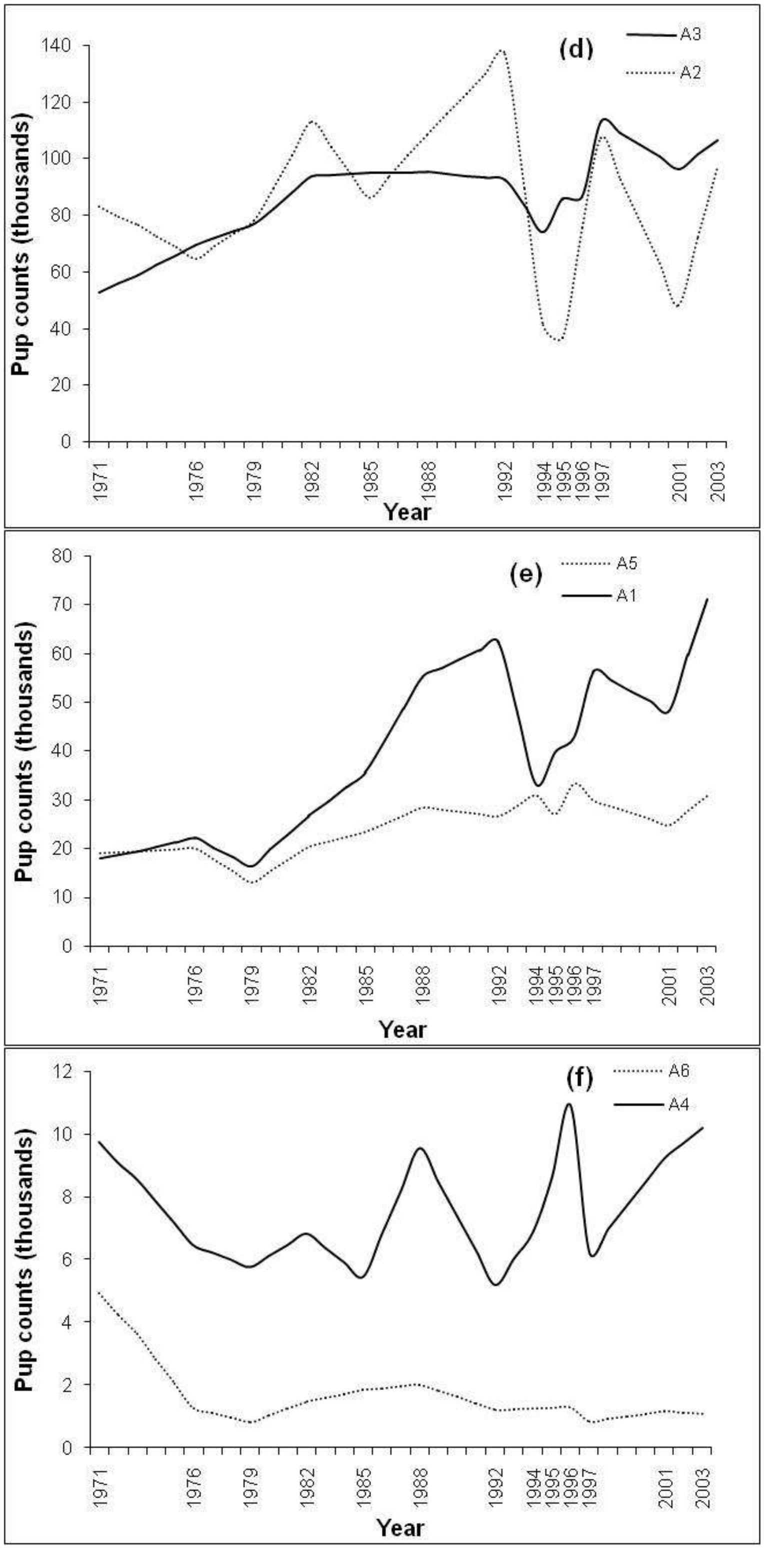

Figure 3 (cont.)

Appendix 1 Cape fur seal pup counts from aerial censuses (1970–2003). Under-lined years were full census years, blocked cells indicate missing or inadequate counts for which proxy values were determined. In all other blank cells, counts were not made. Included are data previously presented in Shaughnessy (1987), Oosthuizen and David (1988), Wickens *et al.* (1991), Butterworth *et al.* (1995), and recent census results.

Colony :	**1970**	***1971**	**1972**	**1973**	**1974**	**1975**	**1976**	**1977**	**1978**	**1979**	**1980**	**1981**
Cape Frio		0							0			
Cape Cross		17839					22097			16327		
Hollams Bird Is		5042					2772					
Mercury Is		0					0			0		
Marshall Reef		755					378	258				
Staple Rock		2910					2114	2472		1236		
Boat Bay Rock		1691					978	971		528		
Dumfudgeon Rock		2875					779	920		616		
Wolf Bay		[b]7443		[a]8805			[b]15017		17852			
Atlas Bay		[b]8879		[a]23295			[b]23759	36453	55852			
Long Is		12228					9840		13361	12252		
Albatross Rock		3722					2393			4632		
Black Rock							205			278		
van Reenen Bay		3243					[a]3208			3591		
Sinclair Is		15772					10879	9461		11370		
Lion's Head		2769					3248					
Kleinsee		30450	27776				52075			59165		
Elephant Rock		2496	1095			1629	1398			1826		
Bird Is, LB												
Paternoster Rock												
Jacob's Reef		4808	3376				3772					
Robbesteen		2427					1273			473		
Seal Is, FB	[a]14449						12199	12297		8188		8574
Geyser Rock		2680				4952	6638			4099		6137
Quoin Rock		3746			1730		1090	765		630		
Seal Is, MB		3237			1262		1176	957		380		
Black Rocks, AB		1703			904		86			442		

(*) 1972 photographs taken on 4–6 December, therefore values are adjusted by factor of 1.5539; (a) considered undercounts because photographs taken in January; (Shaughnessy 1987); (b) considered undercounts because unrealistic in comparison with harvest figures (possibly due to incomplete coverage of colonies).

Appendix 1 (cont.)…

Colony :	**1982**	**1983**	**1984**	**1985**	**1986**	**1987**	**1988**	**1989**	**1990**	**1991**	**1992**
Cape Frio	1			3							477
Cape Cross	26623			35590		37882	55247	51890	44636	65557	61891
Hollams Bird Is	1945						5216	3267			4902
Mercury Is	0		1128	3606	3828	5178	3114	[d]460			35
Marshall Reef				398			666		384		942
Staple Rock				2212			2325		2314		1405
Boat Bay Rock	1167			1618			2066				1240
Dumfudgeon Rock	883			1623			2003		552		1667
Wolf Bay	26669			[c]10616		29454	24548	19286		25680	39534
Atlas Bay	61438			[c]16860		43923	42223	41607			62823
Long Is	13223			12812			22160				20170
Albatross Rock	5254				3331		4354				1715
Black Rock	216		407	202	393	491	439		461		200
van Reenen Bay	4953		6701	4820	6900	6235	5590	4990	5232		5293
Sinclair Is	9419			8011			11139				8703
Lion's Head	1614		1792	1817			3437				6121
Kleinsee		83469		[c]43267	[c]47113	[c]46850	74620	78809	63246	79301	72203
Elephant Rock	2748			2612		3740	3326		3476	3841	2193
Bird Is, LB			0	10	8	8	0	3	7	0	14
Paternoster Rock				127	74	943	1098	1527	1697	1877	758
Jacob's Reef	3132		3270	1086		1971	3886			3606	1265
Robbesteen	929		1515	1616	1368	1575	1224		1487	1722	964
Seal Is, FB	10017		11010	12116	[d]5218	14105	13503	15484	13898	17522	12974
Geyser Rock	9151	6954	8345	9584	8643	10187	12793	10749	9651	11522	11743
Quoin Rock	1074			1644	1496	1756	2041	1676		2367	1834
Seal Is, MB	899				1170			1238			754
Black Rocks, AB	561				808		800				463

(c) Aerial censuses preceded by large male harvests that resulted in breeding disturbance, thereby probably reducing pup production (Wickens *et al.* 1991). (d) Breeding population deliberately disturbed during breeding season therefore pup production reduced (Wickens *et al.* 1991).

Appendix 1 (cont.).

Colony :	**1993**	**1994**	**1995**	**1996**	**1997**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**
Cape Frio		3044	4337	4419	7191				10880		16608
Cape Cross		29990	35498	38564	48993				37394		54546
Hollams Bird Is		961	2026	1827	3478				2285		2305
Mercury Is		0	0	0	0				0		0
Marshall Reef				242	146				106		
Staple Rock				1542	1899				1462		
Boat Bay Rock				693	883				669		
Dumfudgeon Rock					465				1099		
Wolf Bay	28476	9642	9158		36700				15184		29531
Atlas Bay		17031	13581		46225				18193		45155
Long Is		8809	7751	12098	14835				7822		12648
Albatross Rock		2031	1152	2451	2785				1335		
Black Rock		252	210	100	206				84		259
van Reenen Bay		3011	3317	3989	5783				2953		
Sinclair Is		6992	7967	7186	10771				7472		10543
Lion's Head		4501	4623	5529	8308				6163		9603
Kleinsee		59370	69669	69930	87841			91641	79710		80897
Elephant Rock	3813	2110	3092	4074	2165				4293		4398
Bird Is, LB		66	352	314	40				130		592
Paternoster Rock		2476	1932	3233	1200				1014		908
Jacob's Reef		1566	2221	2064	1650						3376
Robbesteen		707	976	1212	1155						908
Seal Is, FB	15235	17144	13528	19396	16806				12298		18339
Geyser Rock	10324	11616	11939	12266	11184				[e]5659		
Quoin Rock	1694	2080	1520	1639	1779				1223		
Seal Is, MB				989	691				658		
Black Rocks, AB				296	142				505		423

(e) Considered undercount due to high altitude of photographs.

CHAPTER 3

A critical assessment of seal-seabird interactions in southern Africa, reflecting on past versus present population size of the Cape fur seal

Abstract

Through predation and displacement, the Cape fur seal *Arctocephalus pusillus pusillus* poses a threat to several seabird species that breed in southern Africa. Measures such as the culling of “problem” seals have been introduced to negate the effects on these species, but there have been calls for stronger measures to be taken against seals. In this review, past evidence for direct impacts of seals on seabird populations was scrutinised. It was found that frequently the interpretation of seabird numerical trends, or of anecdotes on seal-seabird interactions, appear biased against seals. It was mooted that, as with seal-fishery interactions, the conspicuous nature of seals and some of their behaviour may have resulted in their effects on seabird colonies or populations being overemphasised in the past. The poor conservation status of the impacted seabird species has been influenced by numerous factors, foremost of which was human interference and historical bad management practices. Culling or displacing of seals, at any scale, were unlikely to reverse trends in declining populations of seabirds, especially if conducted in isolation of other management actions, such as measures to enhance or expand the breeding habitat of seabirds. Arguments in justification of reducing seal numbers to reduce impacts on seabirds or other marine living organisms, based on speculation of past to present seal population size, were considered in a logical framework and found to be unsupportable.

Keywords: *Arctocephalus pusillus pusillus*, competition, displacement, interactions, predation, management, seabird, southern Africa

Introduction

The Cape fur seal *Arctocephalus pusillus pusillus* has long been a subject of controversy with regard to its impacts (real or perceived) on fishing operations and catches (David 1987, Wickens *et al.* 1992a). Within recent decades, effects of the seals on the conservation status of locally breeding seabird species have also received attention. For example, in the workshop report of the Conservation Assessment and Management Plan (CAMP) for southern Africa seabirds held in Cape Town in 2003 (du Toit *et al.* 2003), the Cape fur seal *Arctocephalus pusillus pusillus* was ranked as the animal posing the greatest threat to the conservation status of locally breeding seabirds, in terms of competition for breeding space and predation. These direct threats were distinguished from indirect threats, such as potential competition for prey. Also, in numerous articles in scientific and other literature, mention was made of the impacts of seals on local seabird individuals, colonies or populations (Table 1). This article critically reviews the interpretation of anecdotes and facts presented in various reports and publications and the scientific basis for some of the conclusions and recommendations which have been reached regarding management of seal-seabird interactions in southern Africa. The emphasis in this review was on the direct impacts of seals on seabirds, as described above, rather than indirect effects, such as competition for prey.

A short backdrop to the past management of the islands situated off the coast of South Africa and Namibia is provided here. There are at least 30 islands with an area greater than 0.5 ha, the largest being Robben (500 ha), Dassen (220 ha) and Possession (90ha) Islands (see Figure 1) (Rand 1963a, b). Whereas seal and seabird colonies co-existed on many of the islands three to four centuries ago at the time when Europeans began to make their mark in the region (Shaughnessy 1984), the physical characteristics and faunal composition of many of the islands have altered radically since. Between the 17th and the early 20th centuries, seals were hunted to extinction at many of the larger islands including the afore-mentioned three and at least 20 other islands (Shaughnessy 1982). Many of these sites were subsequently manned on a year round basis and managed for the production of seabird products such as guano and eggs, to the exclusion of seals. Hence, it became customary to refer to “seal islands” and “seabird islands” (or “guano islands”), exclusively. The former included mainly smaller islands of 2 ha or less in area, which were inaccessible or unprofitable for sealers or guano collectors to exploit (Rand 1952a, Shaughnessy 1984). Some of the better known seabird islands include Bird (Nelson Mandela Bay), Dyer, Dassen and Malgas Islands in South Africa, and Ichaboe, Mercury, Seal (Lüderitz Bay), Penguin (Lüderitz Bay) and Possession Islands in Namibia (Figure 1). As the guano supplies dwindled, especially during the last half of the 20th century, personnel were gradually withdrawn from the seabird islands (Shaughnessy 1984) and by the end of the century, year-round human occupation had ceased on all but a few of them, such as Ichaboe, Mercury, Possession, Dassen and Dyer Islands. With many of locally breeding seabird populations having declined in recent decades (Kemper *et al.* 2007a), the focus has shifted from safeguarding the islands for production of seabird products, to research and management for conservation (e.g. DEAT 2007, Kemper 2007a).

Competition for space

Background

Humans, by scraping accumulated deposits of guano from the surfaces of islands off the southern African coast between the 18th and 20th centuries, removed most of the formerly available refuges and nesting material of many seabird species from the islands (Williams 1988, Shaughnessy 1984). This has negatively affected the breeding success of several seabird species in a number of ways (Frost *et al.* 1976, Shelton *et al.* 1984, Crawford *et al.* 1989). For example, parts of Cape gannet and African penguin colonies became basin-shaped as a result of guano collection, causing rainwater to accumulate and flood nests. Exposure of penguin chicks and nesting adults to incoming solar radiation was increased, leading to increased chick mortality (e.g. from heat stress) and nest abandonment. Eggs and chicks also became more vulnerable to predators such as gulls, and to crushing, e.g. by seals where they occur. All the above have placed breeding seabirds at a disadvantage, relative to seals utilising the same locations. It has been speculated that the removal of the guano cap at some islands may be to the benefit of seals, through allowing them to penetrate the interior of the island and so avoid the heavier pup mortality associated with breeding close to the water's edge (Shaughnessy 1984).

In the CAMP workshop report (du Toit *et al.* 2003), various management suggestions were put forward to mitigate the problem of seabirds being out-competed for breeding space by seals. These included, *inter alia,* removal of seals from seabird islands by constant disturbance and elimination of persistent animals, and preventing the re-establishment of new seal colonies at islands. Two degrees of seabird "displacement" by seals were specified, namely total and partial displacement. To "displace", by definition, means to remove, expel, force or drive out from the proper place, or in a broader sense, to take the place of. Seal Island (presumably the one in

False Bay), Albatross Rock and Elephant Rock (Figure 1) were given in the CAMP report as examples of locations where seabirds have been totally displaced by seals. The displacement of gannets and penguins to sub-optimal breeding sites by seals re-colonising Mercury Island during the 1980s, was given as an example of partial displacement. Also included under the latter definition was the disturbance of courtship, disruption of breeding attempts, deterrence of recruits, blockage of landing sites and access paths, and attraction and/or support of large numbers of predators such as killer whales *Orsinus orca* and kelp gulls *Larus dominicanus*.

A further literature search found numerous reports and publications which implicate seals in “displacing”, “evicting”, “excluding”, “competing with”, “encroaching upon” or “preventing from settling”, various seabird species, at several locations. There are too many such references to discuss each one at length (Table 1), therefore this review shall concentrate mainly on those provided as examples in the CAMP report.

Case studies

Albatross Rock

From the records of the early sealers, Shaughnessy (1984) determined that seals were present on Albatross Rock in the 1820s, but they were extirpated by seal hunters some time before 1843, the time of the guano boom in southern Africa. Seals were apparently absent from the island until the 20th century, when they were first observed again in 1946 (Rand 1972). Following re-colonisation, there was already a thriving breeding colony by 1951, at which time annual sealing by Government sealers commenced there, continuing to 1982. During this time an average of about 915 seals were killed by sealers at the island each year (Wickens *et al.* 1991).

There is only a single record from the 19th century of the seabird fauna on the island, by Captain John Spence (cited by Shelton *et al.* 1984), who stated that in about 1885 “…penguins and duikers (cormorants)…” (but no seals, which had already disappeared from there) were present. This was the only known observation of African penguin *Spheniscus demersus* there. During a survey of the island in 1956, no penguins were found (Rand 1963b), nor has a penguin colony established there subsequently (Shelton *et al.* 1984, Crawford *et al.* 1995a). However, while Crawford *et al.* (1995a) suspected that Albatross Rock formerly may have been the site of a penguin breeding colony, the record of penguins there in 1885 was not evidence that they bred there. It was possible that the penguins sighted then were merely visiting and that cormorants were the main producers of guano at the island – three species of cormorants, namely the Cape cormorant *Phalacrocorax capensis*, bank cormorant *P. neglectus* and crowned cormorant *P. coronatus*, were still breeding in small numbers there around the end of the 20th century (Crawford *et al.* 1995a, Kemper *et al.* 2007a).

Even if a penguin breeding colony did previously exist at the island, there was no evidence that it was still there at the time the island was re-colonised by seals, in 1946 or before. Such a colony may have gone extinct at any time after 1885, for several possible reasons. Not least of these was the disturbance and habitat destruction associated with guano exploitation, which continued at the island at least into the early part of the 20th century, and which, along with other forms of seabird exploitation such as egg collection, has been cited as the principal cause of the general decline in African penguin numbers during the first half of the 20th century (Frost *et al.* 1976). If a penguin colony did occur concurrently with the seal colony which was re-established at Albatross Rock in the 20th century, it is fair to say that the penguins would probably have been at a competitive disadvantage with regard to space, on account of the habitat alterations caused by guano collections. However, it was possible that disturbance associated with annual winter sealing after 1950 would have contributed at least as much to the failure of such a penguin colony, as the seals themselves.

Therefore, although it is indisputable that seals are currently the predominant wildlife at Albatross Rock, following their re-colonisation of the island in the 20th century, it is equivocal whether a breeding colony of African penguins did disappear from the island and if they did, how much of a role seals would have played in their disappearance.

Elephant Rock

According to anecdotes, seals were breeding at Elephant Rock in the 1820s, when the first recorded seal harvests occurred there (Shaughnessy 1984). Sealing continued there, along with regular collections of guano and other seabird products, after guano was discovered there in 1845. Unlike Albatross Rock, seals were apparently never extirpated from the island due to human activities, although their numbers were considerably reduced at times. From 1950 to 1976, when sealing was eventually discontinued at Elephant Rock because of the reduced size of the herd (Shaughnessy 1984), an average of about 920 seals were killed per year at this location.

As in the case of Albatross Rock, there is only one reference to the African penguin occurring at Elephant Rock (cited by Brooke 1986) and no evidence that they ever bred there (Shelton *et al.* 1984, Crawford *et al.* 1995a). In 1992, when a landing was made on the island, seals were the dominant wildlife and some Cape cormorants and crowned cormorants were breeding there, but there were no signs of penguins, or of recent breeding by penguins (Crawford *et al.* 1995a). Crawford *et al.* (1995a) concluded that seals may have "precluded settlement of penguins at Elephant Rock". There is incongruity between this statement and "total displacement" (of penguins by seals) as stated in the CAMP report, even in the broadest sense of the latter term. Moreover, as in the case of Albatross Rock, if penguins did previously breed at Elephant Rock, their disappearance could have been influenced by other factors besides encroachment by seals. These include guano scraping and exploitation of eggs, as well as disruption caused by sealing.

Seal Island (False Bay)

Since the arrival of Europeans in the Cape, at least three seabird species were known to have ceased breeding at Seal Island. These were the Cape gannet *Morus capensis*, the great white pelican *Pelecanus onocrotalus* and the kelp gull (Shaughnessy 1984).

On the first recorded visit to the island, in November 1687, Simon van der Stel indicated that gannets were abundant there and that his men collected three baskets full of eggs (cited by Shaughnessy 1984). This was the only record of gannets at the island, for which an early name was Malgas Island, meaning Gannet Island (Shaughnessy 1984). It has been questioned whether the gannets present were perhaps only roosting there and the party perhaps mistook gull eggs for gannet eggs (Shaughnessy 1984). However, gannets rarely roost at locations where they do not breed therefore it has been assumed that they did breed at Seal Island, co-existing with the seal colony, at the time of van der Stel's expedition (Crawford *et al.* 1983, 1994). This was not unlikely, considering that the terrain at Seal Island is amenable to gannets breeding, and that seals and gannets were known to co-exist at other islands at the time Europeans began exploring and exploiting them (Shaughnessy 1984). Gulls and a large seal population were also noted by van der Stel's party.

After van der Stel's visit, there was no information on the fauna of Seal Island until the reports of several travellers that visited it around the end of the 18th century. From their accounts (cited by Shaughnessy 1984), it was apparent that seals were abundant on the island at this time, and were being harvested. Penguins were also reported to be present, but gannets were probably absent from the island by this stage, as they were not recorded in any of the accounts. However, it was highly unlikely that the loss of gannets from the island between 1687 and the end of the 18th century was directly related to seals. Guano exploitation at the island, and the associated modification of the terrain which supposedly would have given seals a competitive advantage with regard to breeding space, only commenced later, in 1845 (Shaughnessy 1984). Continued exploitation of gannet eggs, in the vein of van der Stel's party, and/or disturbance associated with seal harvesting (sealing), could have contributed to the gannets' disappearance, if indeed they did ever breed there.

By the mid-1800s, seals had been considerably reduced and possibly exterminated at Seal Island, on account of unsustainable sealing and perhaps interference associated with guano scraping activity (Rand 1951, Shaughnessy 1984). Only after a sustained period with no sealing activity (1942–1950) and the cessation of guano collections in 1949, did seal numbers again begin to increase there. According to Rand (1963a), seals had "over-run" the island by 1955. The growth in seal numbers was apparently detrimental to the breeding success of kelp gulls, which no longer nest on the island (Rand 1951, Shaughnessy 1984), and may have caused the failure of the great white pelican colony (Rand 1963a, Shaughnessy 1984). The pelicans, which were first noticed there in the 1930s, were absent by 1967. However, Rand (1951,1963a) acknowledged that seals on the island tended to avoid the pelican breeding colony and that other factors may have contributed to the failure of the pelican breeding colony, besides the activities of seals. These include the disruptive effects of winter sealing at a crucial time of the pelicans breeding cycle, as well as other interference. Between 1951 and 1975, Government sealers were killing seals at the island at a rate of about 2 900 per year (Wickens *et al.* 1991). This must have caused considerable disturbance not only to the pelicans, which lay their eggs in winter and abandon breeding for the year if their attempt was unsuccessful, but to other winter breeders present on the island such as the African penguin. The "other interference" referred to by Rand apparently include the use of the island for target practice during naval manoeuvres, and riflemen shooting at seals in the seal colony (Rand 1963a, Crawford *et al.* 1994). Rand (1951) describes one pelican breeding season in which human interference caused the decimation of all pelican eggs and all but four pelican chicks, by gulls.

Therefore, of the three species which have reportedly ceased to breed at the island since the arrival of Europeans, it was unlikely that the loss of gannets was directly connected to seals and there was no evidence to support that it was, while human interference was likely to have contributed at least as much as seals, if not more, to the demise of the pelican colony. Seals are undoubtedly the predominant wildlife at the island currently, though small breeding populations of African penguin, Cape cormorant, bank cormorants and white-breasted cormorant *P. carbo* persist there (Dyer and Underhill 2003).

Mercury Island

According to the records of early sealers (discussed in Best and Shaughnessy 1979), a seal breeding colony existed at Mercury Island in the 1820s. This colony was eradicated before guano was discovered on the island in the 1840s. The island was managed for guano collection and permanently staffed until 1973, during which time seals were kept off the island (Crawford *et al.* 1989). Human presence on the island was sporadic after 1973 and a few non-breeding seals were first seen on the island in 1981; this rapidly built up to about 16 000 seals within the next five years (Crawford *et al.* 1989). The seals commenced breeding there in 1984 and pup production had risen to over 4 000 by 1986. Crawford *et al.* (1989) proposed that the source of the seal influx was probably the large Atlas Bay and Wolf Bay breeding colonies situated on the mainland south of Mercury Island. Summertime sealing operations that extended well into the breeding season at these colonies in the 1980s, caused severe disturbance to pregnant females and those with newborn pups (Best 1990), probably resulting in the re-location of many seals to Mercury Island and elsewhere.

During the period of seal occupation, the space on the island utilised by three of the resident seabird species, namely Cape cormorants, bank cormorants and African penguins, was reduced and a small number of gannets were also reported to have been partially displaced by the seals (Crawford *et al.* 1989, David 1989). Declines in breeding numbers or active nests of penguins, bank cormorants and Cape cormorants during this period was attributed to the effects of seals (Crawford *et al.* 1989). Human occupation of the island was resumed as from 1985 in the interests of seabird conservation and seals were cleared off (Crawford *et al.* 1994, Roux and Sakko 1997). Following removal of the seals, penguin and bank cormorant active nests once again increased in the early 1990s (Crawford *et al.* 1999, 2001); this has been taken as evidence that the seals did negatively affect breeding in these species, and of the success of the seal disturbance program (Crawford *et al.* 1994, du Toit *et al.* 2003).

The closest bank cormorant and penguin colonies to Mercury Island exist at Ichaboe Island, 65 km to the south. It is interesting that numerical trends of these two species, as given in Crawford *et al.* (1995b) and Crawford *et al.* (1999), were not dissimilar between the two islands for the period discussed above (Figures 2 and 3). It must be noted that at each of these islands, only one count of active penguin nests was conducted for each of the periods 1976–1980 and 1981–1985 referred to in Figure 2 (Crawford *et al.* 1995b). It follows that any trends based on such counts assume synchrony in breeding effort between years. However, according to Kemper *et al.* (2007b), the penguin breeding season in Namibia tends to not be well synchronised. This, together with a prolonged breeding season, makes single counts of active nests a poor proxy of the size of the breeding population and potentially could lead to gross misinterpretation of trends (Kemper *et al.* 2007b). Furthermore, counts of bank cormorants at Mercury Island up to 1987 were conducted in November or early December, which was earlier than the typical breeding peak for this species in Namibia (J Kemper pers. comm.). As bank cormorant numbers may fluctuate widely early in the breeding season (J Kemper pers. comm.), the trend for Mercury Island in Figure 3 also needs to be interpreted with caution. Below, the discussion focuses on the interpretation of the trends rather than the reliability of the counts, making the assumption that the observed trends were true.

The declines at Ichaboe Island between the late 1970s and the mid 1980s that are evident in Figures 2 and 3 were not attributable to seals because the island was manned at the time and there was no seal encroachment. In fact, the declines have been attributed to possible disturbance caused by guano collectors there before 1986 (Crawford *et al.* 1995b). However, when one considers the comparable trends for the two species between the two locations, it does not seem improbable that a common factor may have played a role in these trends. In 1984, a severe Benguela Niño event occurred in Namibia, drastically decreasing the productivity of the region and depleting the stock sizes of several prey species (Gammelsrød 1998). It is therefore quite conceivable that food shortages contributed to the declines in the numbers of active nests at both islands, by causing abandonment or deferral of breeding. There were also downward trends at the two other bank cormorant colonies in the region for which counts were available over this period, namely Seal Island and Penguin Island at Lüderitz (Figure 3).

The downward trend in the number of Cape cormorants at Mercury Island during the 1980s was also similar to other locations in the region where no seal encroachment occurred at the time, including Seal and Penguin Islands (Lüderitz) and Ichaboe Island (Figure 4) and was therefore consistent with the general reduction of Cape cormorant numbers in southern Namibia during the 1980s and 1990s. This decline has been linked to depletion of prey stocks, including anchovy *Engraulis encrasicolus* (Crawford *et al.* 2007). Therefore, while it was possible that seals played a role in the perceived reduction in numbers of three seabird species at Mercury Island in the 1980s through encroachment (Crawford *et al.* 1989), the observed numerical trends of conspecific seabirds from other locations in the region where no seal encroachment occurred, indicate that another factor, in common throughout the region, was perhaps even more important. This factor was likely to have been the wide-scale decline in prey stocks documented for the region during the relevant period.

Further examples and discussion

According to Crawford *et al.* (1989), the significance of the displacement of seabirds by seals at Mercury Island was that the effect of seal encroachment on the distribution and abundance of seabird species could be monitored, whereas previously, documentation of seal displacement of seabirds had been largely anecdotal. Reference to evidence as “anecdotal” can imply that it is subjective or unreliable; considering the examples discussed above, the term seems appropriate because in some cases there was little or no evidence to support the contention that seals played a significant role in the disappearances of seabird species.

Other cases listed in Table 1 have similar relevance. For example, at Sinclair Island (Figure 1), according to at least one record (cited by Shelton *et al.* 1984), both seals and penguins occurred historically. In 1940, a concrete wall was erected around the area utilised by penguins for breeding (the “penguin flats”), apparently to exclude seals. However, between 1956 and 1967, gaps appeared in the wall, opening the area up to seals, which by 1967 outnumbered penguins in the area (Shaughnessy 1980). Over this period, the penguins declined drastically at a rate of about -7.5 % per year (Figure 5). As no seals occurred at neighbouring Plumpudding Island (2.5 km from Sinclair Island) at the time, and according to the counts, the penguin population there was more stable over the same period, having declined by only 2.0 % per year, it has been inferred that displacement by seals was probably the primary cause of the decline in penguin numbers at Sinclair Island (Shaughnessy 1980, Shelton *et al.* 1984, Crawford *et al.* 1994).

Also between 1956 and 1967, the penguin populations at Possession Island and North Reef, which are close together but approximately 80 km north of Sinclair and Plumpudding Islands, were estimated to have declined at rates of -6.7 % and -7.4 % per year, respectively (Figure 5). These rates were similar to the decline at Sinclair Island over this period. Seal encroachment was not responsible for the declines at Possession Island and North Reef because seals did not occur at these islands at the time. Shelton *et al.* (1984) also considered it unlikely that food shortages were accountable, because the period in question was before the collapse of Namibia’s sardine *Sardinops sagax* stock in the 1970s (Shelton *et al.* 1984). Instead, it has been put forward that sealers, who used Possession Island as a head-quarter at the time, might have caused disturbance that contributed to the downward trends at this pair of islands (Crawford and Shelton 1981, Shelton *et al.* 1984).

Until 1960, temporary accommodation was also provided to sealers at Sinclair Island, in two concrete buildings situated within the penguin enclosure (Shaughnessy 1980) and it is feasible that sealers staying there would have caused disturbance to penguins, and may also have utilised penguin eggs for food. Furthermore, sealing operations occurred annually at the island between 1956 and 1967, and the sealers would use the penguin enclosure to secure seals that were herded in through the gaps in the wall, before dispatching them with clubs (Shaughnessy 1980). On average, 4 260 seals were killed at Sinclair Island during each sealing season between 1956 and 1967, with over 8 000 seals being killed in both 1956 and 1957 (Wickens *et al.* 1991), representing over 80 % of the average number of pups counted there during later (1972–2004) annual aerial censuses (based on Chapter 2). Sealing at this scale, and particularly any such activity within the penguin enclosure, would have been damaging to the penguin colony. This was especially so considering that penguins breeding in the northern Benguela Current Ecosystem have a primary incubation peak in winter (Kemper 2006), the time of the year when the seal pups are clubbed.

Therefore, an alternative case can easily be made to the one stating that seal encroachment was accountable for the decline in penguin numbers at Sinclair Island (where seals breed) between 1956 and 1967, because penguin numbers at the neighbouring island (where seals do not occur) were more stable over this period. It would state that because penguin numbers declined at similar rates at three different colonies which were affected by sealing or other activities of sealers (Sinclair Island, Possession Island and North Reef), the trends at these colonies could be attributed to direct human interference. Sealing operations also occurred regularly during the 20th century at several other locations where penguins declined drastically in numbers or disappeared. These include, in addition to Elephant Rock, Albatross Rock and

Seal Island in False Bay: Seal Island in Mossel Bay, Quoin Rock, Geyser Rock, Jacob's Reef, and Long Islands (Figure 1).

Considering the cases presented above, past evidence demonstrating competitive effects of seals for space on the numbers and breeding success of seabirds was generally inconclusive. It seems that the interpretation of anecdotes or, in the case of Mercury Island, actual numerical trends, have invariably attributed the loss of (or the lack of) seabirds at locations to encroachment by seals, while other potential causes such as adverse feeding conditions or human interference, were frequently disregarded. Even in the well documented case of Mercury Island, for which encroachment of seals into the seabird colonies was diligently mapped (Crawford *et al.* 1989), it must be kept in mind that the large scale influx of seals to the island was itself probably a direct result of human interference. The scale of the influx of seals at this location, the numbers of seabirds involved and the rate at which they were encroached on, can therefore not be seen as typical. Interestingly, according to counts of active nests (Namibia Ministry of Fisheries and Marine Resources unpubl. data) since the cessation of sealing operations at Sinclair Island in the early 1980s (Wickens *et al.* 1991), the penguin population has remained stable there. On the other hand, the penguin population at Plumpudding Island fluctuated substantially, declining by 99 % between 1988 and 1990 before recovering to about two thirds of its 1988 level by 1999. If anything, this illustrates the need for caution when attributing cause for seabird population trends, as well as the risk attached to not considering further than the most visible potential cause, which is frequently the Cape fur seal.

Predation

Background

According to Crawford and Robinson (1990), records of isolated incidents of predation on seabirds by Cape fur seals date back to at least the early 1900s. Studies during the past decade have shown that the predation levels at a few seabird breeding colonies, including at Dyer Island, Malgas Island, Lambert's Bay and Ichaboe Island, were substantial (Marks *et al.* 1997, du Toit *et al.* 2004a, Ward and Williams 2004, Makhado *et al.* 2006). The species most at risk were the African penguin, the Cape gannet, the bank cormorant and the Cape cormorant (see Table 1), the conservation status of which, according to IUCN criteria, range from vulnerable to endangered (Kemper *et al.* 2007a).

Of the cormorants, it is newly fledged birds which were taken (Marks *et al.* 1997, du Toit *et al.* 2004a, Ward and Williams 2004). Most gannets taken were also newly fledged chicks, but adults were also attacked at the time of nest building (Ward and Williams 2004). While the majority of attacks take place in the sea near by seabird colonies, some have been observed on shore (Rebelo 1984, Crawford and Cooper 1996, Wolfaardt and Williams 2006). In most cases, at least part of the prey is eaten, although there have been observations of seals attacking seabirds without consuming anything (Cooper 1974, Marks *et al.* 1997, du Toit *et al.* 2004a). Diet studies have indicated that seabirds contribute negligibly to the diet of the seal population as a whole, and were not a normal prey item of seals at their usual foraging grounds (David 1987, Castley *et al.* 1991, David *et al.* 2003, Mecenero *et al.* 2005). Predation of seabirds by seals is rarely, if ever, observed in the open ocean (J-P Roux pers. comm., MA Meÿer pers. comm.) and seems to occur almost exclusively in the vicinity seabird breeding colonies, with relatively few individual seals responsible, these being generally juvenile and sub-adult male seals (Shaughnessy 1978, Navarro 2000, David *et al.* 2003, du Toit *et al.* 2004a). However, even if only a few individuals were responsible for the seabird predation, these can potentially have a significant impact on local seabird populations, as a single seal may kill many seabirds in one day (Williams 1988, du Toit *et al.* 2004a). This was illustrated by the removal of one individual male seal at Ichaboe Island in Namibia in the 1993, resulting in a sharp subsequent decline of the rate of predation on adult cormorants there (du Toit *et al.* 2004a). A perception that both the numbers of seal individuals preying on seabirds, and the levels of seabird predation have increased since the 1980s (du Toit *et al.* 2003, Wolfaardt and Williams 2006, Makhado *et al.* 2006) has resulted in heightened concern regarding the threat that this interaction poses to the conservation status of local seabirds.

Why the perceived increase in seal-seabird predation rates?

A few theories have been put forward to explain the observed increases in seal-seabird predation at several islands off South Africa and Namibia. They include the following:

(a) Depletion of “regular” prey of seals (pelagic shoaling fish, other fish and squid), due to fishing activities or environmental variability, could conceivably cause some seals to switch to “alternative prey” such as seabirds (Marks *et al.* 1997, Makhado *et al.* 2006). Conceivably, the marked eastward shift in the distribution of South Africa’s sardine stock which has taken place since about 2000 (van der Lingen *et al.* 2005, 2006), could have had such an effect on seals along the west coast of the country (Makhado *et al.* 2006). However, at subantarctic Marion Island, for example, numerous incidents of predation by subadult and adult male Antarctic fur seals *A. gazella* on macaroni penguins *Eudyptes chrysolophus* and king penguins *Aptenodytes patagonicus* were being observed (Hofmeyr and Bester 1993, pers. obs. in 1995–1998) while the seal population was undergoing a rapid rate of increase of c. 17 % per annum (Hofmeyr *et al.* 1997, 2006), indicating that their regular prey were not limited. Similarly, while the Antarctic fur seal population at another subantarctic location, South Georgia, was recovering from overexploitation, at an accelerated rate due possibly to the absence of competition from whales for their main prey, Antarctic krill *Euphausia superba* (Croxall 1992), subadult male seals were frequently seen preying on macaroni penguins (Bonner and Hunter 1982). Therefore, characteristics of predation involving other populations of fur seals and penguins suggest that high levels of seal-seabird predation can occur irrespective of the availability of regular prey species.

(b) It has been suggested that following the growth in Cape fur seal numbers which took place during the 20th century (Butterworth *et al.* 1995), the increased number of seals may have led to increased predatory interactions with seabirds (Ward and Williams 2004, Wolfaardt and Williams 2006, Makhado *et al.* 2006). However, according to aerial censuses of seal pup production, most of the growth in the seal population in South Africa occurred at Kleinsee (Chapter 2), a mainland colony some 300 km north of Lambert’s Bay (Figure 1), the location of the northern-most of South Africa’s important seabird breeding colonies (Bird Island). The seal colonies situated on islands, which are generally situated in closer proximity to major seabird breeding colonies than mainland colonies, showed comparatively little increase since the initiation of the census time series in the 1970s (Chapter 2). Nevertheless, a few new seal colonies have been established on South African islands since the 1980s, including at Bird Island in Lambert’s Bay, Paternoster Rocks and more recently, Vondeling Island (Figure 1). Seals may have dispersed to these locations in response to overcrowding, human disturbance at established colonies, the availability of “regular prey” (Oosthuizen and David 1988), or some combination of these effects. Whatever the cause(s), such localised increases would have served to multiply the numbers of seals in close proximity to major seabird breeding colonies such as at Lambert’s Bay and Malgas Island, where increases in occurrences of seal-seabird predation have subsequently been documented (Ward and Williams 2004, Wolfaardt and Williams 2006, Makhado *et al.* 2006). Similarly, in Namibia, where seals have been prevented from re-colonising their former breeding habitat at Ichaboe Island on account of guano collection and seabird conservation motives, seals have inhabited a neighbouring rock called Little Ichaboe (du Toit *et al.* 2004a), where they were first reported in 1978 (Oosthuizen and David

1988). The numbers of seals that can inhabit this rock are trivial in terms of the seal population size, but individuals residing here are the most obvious source of predation on seabirds breeding at Ichaboe Island.

Therefore, localised increases of seals, leading to the formation of seal colonies near major seabird breeding colonies, may have caused an increase in seal-seabird predation. Earlier in the 20th century, seals would have been prevented from settling on an island such as Vondeling Island, as it was manned full-time to safeguard breeding seabirds for the exploitation of guano and eggs.

(c) David *et al.* (2003) proposed that increased awareness of seal-seabird predation may also have played a role in the perceived increase of this interaction. They suggested that frequent seal-seabird predation around seabird colonies may have been a normal occurrence in the past, but escaped attention due to the paucity of observers. For example, Cooper (1974) witnessed several seal-seabird predation events around Dassen Island as far back as 1971–72 and before this, there were accounts of male seals preying on penguins at Halifax and Dyer Islands, in 1957 and 1937, respectively (Rand 1959). Increased awareness of the issue may therefore have come about through the shift in emphasis regarding the management of seabirds, from exploitation of seabird products, to conservation and ecotourism (e.g. DEAT 2007).

(d) In the past, culling of seals seen preying on seabirds may have reduced incidence of this behaviour, relative to the period since the 1980s (Makhado *et al.* 2006). Several of the headmen who manned the islands in South Africa up to the 1970s or 1980s, while the islands were still being farmed for guano, were armed with .303 rifles and ammunition, and would shoot at seals that were seen preying on seabirds (Makhado *et al.* 2006, PB Best pers. comm., J Kemper pers. comm.). This could have prevented the behaviour from developing in individuals, or being learned by other seals. Indeed, it has been proposed that attacks on seabirds by individual Cape fur seal males may begin either as play behaviour or as opportunistic hunting, but soon develops into a habit, with seabirds eventually forming a large part of the diets of certain individuals which end up specialising in seabird predation (du Toit *et al.* 2004a). There were also accounts of young seals associating closely with older seals as the latter prey on seabirds. The young “novices” observe and mimic the predatory behaviour of the older seals, and afterwards play with the remaining carcass (Marks *et al.* 1997). The implications of seals learning to prey on seabirds through play and through observing other seals hunting seabirds is that the behaviour may easily propagate within local seal populations, and through dispersal of individuals be spread to individuals in other areas. This may be what has occurred since the cessation of permanent human occupation at most of the seabird islands.

It would be extremely difficult to disprove any of the above theories; in fact, it can be expected that some combination of them has given rise to the perceived increase in seal-seabird predation since the 1980s. Of relevance is that, based both on the fact that attacks appear to be limited to a certain sex-age component of the seal population and the model of behavioural development and spread given in the previous paragraph, incidence of seal-predation could proliferate irrespective of trends in the overall size of the seal population.

Case study – Lambert's Bay

The penguin and gannet colonies at Lambert's Bay make for an interesting case study of predation. Ward and Williams (2004) estimated that seal predation was the cause of more than half of the mortality of fully-feathered (i.e., excluding downy chicks) seabirds (gannets, cormorants and penguins) at Bird Island, an island which is presently connected to the town of Lambert's Bay by a causeway. In 2005/2006, the gannets at the island abandoned their breeding attempt. This was blamed on night-time attacks by seals on gannets within the gannet colony, behaviour which had not been recorded before (Wolfaardt and Williams 2006). Apart from conservation concerns – the Cape gannet is ranked as "vulnerable" (Kemper *et al.* 2007a) and there are only six extant breeding colonies of which three are in decline (Crawford *et al.* 2006) – the desertion of the colony by gannets was cited as a commercial crisis for businesses in the town itself, due to loss of tourist revenue (Wolfaardt 2006). Also, based on the rate of seal-penguin predation observed between 1997 and 2000 at the same location, Crawford *et al.* (2001) estimated that the local penguin colony was heading for extinction. The above threats were cited as justification for management intervention regarding seal-seabird interactions at Lambert's Bay (David *et al.* 2003, Ward and Williams 2004, Wolfaardt and Williams 2006).

In the first decade of the 20th century, Bird Island in Lambert's Bay was almost exclusively a penguin colony, but by the 1950s, there were only about 500 adult penguins remaining (Shelton *et al.* 1984). African penguin numbers declined generally in southern Africa during this period, with egg collecting and guano-scraping thought to have been mainly responsible (Frost *et al.* 1976). In addition to disturbance effects and removal of refuges and nesting material normally associated with guano scraping, the central area of the island at Lambert's Bay was paved with flat stones to facilitate the process. The flat area would have favoured gannets, which were first noticed at this location in about 1912 (Crawford *et al.* 1983), at the expense of penguins, which prefer more rugged terrain. Indeed, the gannet colony increased rapidly and was thought to have influenced the decline of penguins by displacing them from breeding space (Shelton *et al.* 1984). However, even though levels of seabird exploitation (including guano and egg collection) in southern Africa had abated by the second half of the 20th century, the decline in penguin numbers did not stop, including at Lambert's Bay where there were fewer than 70 adult penguins by 1978–79 (Shelton *et al.* 1984). Continuation of the decline was attributed to the stock collapse of sardine, favoured prey of the African penguin, due to over-fishing after the 1950s (Shelton *et al.* 1984). Despite a recovery in South Africa's pelagic prey stocks after the 1980s (van der Lingen *et al.* 2006), however, the penguin breeding colony at Lambert's Bay further declined and has apparently been extinct since 2005 (Crawford *et al.* 2008a).

Seals first began hauling out in numbers at Lambert's Bay in the mid 1980s (Oosthuizen and David 1988), therefore it improbable that seals could have been a significant factor in the decline of penguins at Lambert's Bay before this time, though they may have played a role in the demise of the colony subsequently. However, several other factors besides seals could have influenced the trend of the penguin breeding colony at Lambert's Bay since the 1980s. Because the island is so close to the mainland and has been connected to it via a causeway since the 1970s, the eggs and chicks of penguins and the other seabird species present were vulnerable to predation by land-based predators, including indigenous (mongooses) and feral (rats, dogs and cats) mammals (Frost at al. 1976, Ward and Underhill 2002), as well as gulls, which have proliferated because of the scavenging opportunities provided by factories and other outlets. Predation by gulls in particular is exacerbated by any disturbance, such as may be caused by seals or humans. Also, gulls which scavenge at inappropriately disposed carcasses of infected domestic poultry may transmit disease such as avian cholera into seabird colonies (Ward and Williams 2004, Williams and Parsons 2004). Other threats associated with the close proximity of the island to the fishing harbour and town of Lambert's Bay, include oiling (petroleum and fish oil) and exposure to a high concentration of entangling materials and heavy metal and chemical pollutants (Frost *et al.* 1976, Crawford *et al.* 1983), while construction and building renovation within, or in close proximity, to the seabird colonies was known to have caused some displacement and a decrease in numbers of penguins between 1998 and 2002 (Underhill *et al.* 2006). Furthermore, while South Africa's sardine stock recovered in size between the 1980s and the early 21st century, there has been a marked shift in the geographic distribution of the resource southward and eastward from the west coast since about 1997 (van der Lingen *et al.* 2005, Fairweather *et al.* 2006), the cause of which has not been established (van der Lingen *et al.* 2006). Most penguin breeding colonies along South Africa's west and south west coasts have shown declines as this shift has become more acute (Underhill *et al.* 2006, Crawford *et al.* 2008b). As the northern-most penguin breeding colony in South Africa, the Lambert's Bay colony may have been most severely affected by this change. Thus reduced prey availability, either through influencing survival rates or dispersal, may also have played a role in the colony's extinction.

Judging from its downward trend during the 20th century and the multifarious factors potentially limiting recovery, it was unlikely that the penguin colony could have persisted for much longer, even in the absence of seals. In fact, it would be expected that the magnitude of depredations by gulls and terrestrial predators would have become more severe with decreasing penguin numbers therefore extinction of the colony was probably inevitable before the influx of seals to the island in the 1980s. The gannet population at Lambert's Bay has also been subject to the effects described above. Citing seals as the sole cause of the abandonment of breeding by gannets at Bird Island in 2005/2006 was therefore debatable in the light of there being other potential contributing factors. Perhaps most notable among these was prey availability. While gannets can forage more widely than penguins, the foraging behaviour and chick growth of the gannets at Malgas Island (some 110 km south of Lambert's Bay) have been shown to be negatively affected by the movement of pelagic prey to southward and eastward during the past decade (Mullers *et al.* 2007). A potential impact of reduced food availability is increased stress levels, which may have increased the likelihood and rate of desertion by the gannets in response to disturbance within the colony (Wolfaardt 2006). Considering that the abandonment occurred soon after the initiation of management intervention, which consisted of chasing seals entering the gannet colony and shooting of predatory seals to prevent further attacks (Wolfaardt 2006), it was possible that this disturbance may also have contributed to heightened stress among the birds.

Subsequently, a conservation official has been employed to prevent seals from entering the gannet colony and seals observed attacking gannets in the water or on land have been shot. The gannets have returned to breed each year since 2005/2006 and there have been no further large-scale desertions (AB Makhado pers. comm.).

Reflecting on past versus present seal population size

After being severely reduced through over-exploitation, possibly to less than 100 000 individuals (Shaughnessy and Butterworth 1981), the Cape fur seal population increased during the 20th century and is currently estimated to be around 1.7 million individuals excluding pups of the year (Butterworth *et al.* 1995, Chapter 2). It has been proposed by some (e.g. Crawford and Robinson 1990, Makhado *et al.* 2006) that the current population size exceeds the level found before large-scale sealing began in the 17th century. This has been cited as justification for reducing seal numbers, with regard to either reducing the impact of seals on fish resources or seabirds, or both (e.g. RSA 1986, Jürgens 1996, Ward and Williams 2004).

The size and structure of large mammal populations, particularly of marine mammals, are expected to be stabilised by density dependent mechanisms at high population levels (Fowler 1981). Generally, it has been agreed that breeding space or food were the mechanisms most likely to have limited the Cape fur seal population historically (David 1989, Wickens *et al.* 1992b, Griffiths *et al.* 2005). Therefore, those who propose that the carrying capacity of the seal population has been increased in recent times relative to the population's pristine state, propose that the limits of either or both of these mechanisms have expanded. Potentially, this may have come about through (a) the provision of mainland breeding space in protected or restricted access areas with reduced predator populations during the 20th century (David 1989, Griffiths *et al.* 2005); and (b) "free" sources of food supplied by fisheries operations, i.e. scavenging of discarded fish or fish parts, and direct removal of catches from lines or nets (David 1987, Wickens *et al.* 1992a). While there is no way of proving whether the seal population does in fact exceed its pristine size since the historical size of the seal population is unknown (David and van Sittert 2008), the discussion that follows is relevant to the question.

It was considered probable that seals occupied most, if not all the islands along the coast of present day South Africa and Namibia at the time Europeans first arrived in the region (Best and Shaughnessy 1979, Shaughnessy 1982, 1984). It was also generally accepted that when the seal population was still in a pristine state, breeding colonies on the mainland were rare or absent due to predation, including by native hunters (Shaughnessy and Butterworth 1981, Oosthuizen *et al.* 1997). However, due mainly to uncontrolled sealing, seals were absent from most of their former breeding locations, including all the larger islands, by the beginning of the 20th century (Rand 1952a, Shaughnessy 1984). At this time, seal breeding colonies were restricted to small islands all less than 3 ha in area (Shaughnessy 1984). Subsequently, seals have managed to re-colonise a small portion of the islands from where they were previously extirpated, including Sinclair Island, Albatross Rocks, Seal Island in False Bay (Shaughnessy 1984), Mercury Island (Crawford *et al.* 1989) and recently North Reef (Kemper 2006) and Vondeling Island (Mike Meÿer pers. comm.). However, most of the growth in the seal population has occurred at mainland breeding colonies such as Atlas Bay, Wolf Bay and Kleinsee, which were thought not to have existed before the 20th century (Rand 1972, Shaughnessy and Butterworth 1981, David 1989) and Cape Cross, which has been in existence for longer (Rand 1972). Using average values of full aerial censuses of pup counts conducted of mainland and island breeding colonies between 1990 and 2004 (taken from Chapter 2), it was estimated that only a quarter of the current seal breeding population occurs on islands (27.19 % ± 3.74 SD, n = 6 years).

Based on size estimates given in Rand (1963a, 1963b, 1972) and where necessary, area comparisons using Google Earth[5], the total area of the islands where seals were known to have bred previously (Best and Shaughnessy 1979, Shaughnessy 1982, 1984) but are absent from in the present day, is approximately 1 035 ha (n = 20)[6]. The total area of the islands where seals currently breed is only around 25.5 ha (n = 20)[7], of which 62 % comprises Vondeling Island (9 ha) and North Reef (7 ha), islands which were only re-colonised by seals in the 1990s. Therefore, the total area of islands currently occupied by seals is at most about 2.5 % of the total area of islands they occupied historically. Naturally, seals would not have utilised the whole areas of large islands such as Robben Island, Dassen Island or Possession Island, and perimeter, which increases at some fraction of area for most planar shapes, would be a better measure of the breeding space available to seals at the islands. Nevertheless, it can be seen in Figure 6 that the combined coastline length of the large Atlas Bay and Wolf Bay colonies, together for which well over 100 000 new born pups have been counted in some years since 1980 (Chapter 2), corresponds to only about a third of the circumference of nearby Possession Island, where the seal colony is extinct (also shown in the Figure are Long Islands, which at c. 1 ha is typically sized for an island with an extant seal colony). This puts into perspective how vast a seal colony the latter island (the third largest of the islands offshore of South Africa and Namibia) could previously have supported and casts doubt on the notion that the breeding

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[5] http://earth.google.com/

[6] Bird Island in Algoa Bay (19 ha), Dyer Island (20 ha), Pomona Island (3 ha) and Halifax Island (10 ha) are excluded because it is uncertain whether seal colonies occurred there historically (Shaughnessy 1984).

[7] This excludes some small rocks where breeding is known to occur, such as off Cape Columbine and Duikerklip outside Hout Bay.

space was limited in pre-exploitation times because of the relatively small size of the islands (e.g. Griffiths *et al.* 2005). Indeed, when it is considered that a quarter of the current seal breeding population occurs on islands representing just 2.5 % of the total area of the islands previously occupied by seals, the argument that the availability of space for breeding at mainland locations during the 20th century has allowed the seal population to surpass its pristine level, does not seem plausible. Given the above, had breeding space been the most important factor limiting the total seal population size historically, it was likely that carrying capacity would previously have been considerably larger than at the current population size.

On the other hand, if food supply was the most important limiting mechanism historically, then it is expected that the increased removals by commercial fisheries during the 20th century (Watermeyer *et al.* 2008) would have reduced the overall availability of wild prey to top predators such as seabirds and seals and would result in the seal population currently stabilising at below its pristine level. That is, unless there has been significant subsidization of the seal foraging population in recent times by the commercial fisheries operations, as proposed by Williams *et al.* (2000). However, David (1987) and Wickens *et al.* (1992a) estimated that consumption by seals at fisheries operations was negligible in the context of consumption by the seal population, and was therefore unlikely to have played any significant role in population growth.

Based on the previous discussion, neither food nor breeding space was likely to have limited the seal population, historically, to levels below the current population size. Also, the seal population in the present day is subjected to several sources of mortality which would have been absent or insignificant in the pristine population. These include high mortality incurred by first year animals in mainland colonies due to terrestrial predators (Oosthuizen *et al.* 1997) and effects of heat stress (de Villiers and Roux 1992), ongoing sealing in Namibia with current quotas exceeding 80 000 individuals a year (Morton *et al*. 2007) and the numbers of seals which drown incidentally in fishing nets or are deliberately killed by fishermen, which though unknown, are thought to be significant (David and Wickens 2003). When taking all this into account, justifying reductions in seal numbers to reduce impacts on seabirds based on speculation that present numbers exceed historical numbers, is unmerited.

Considerations for the management of seal-seabird interactions

Also of relevance is that seabirds form a negligible portion of the diet of the overall seal population, predation being attributable to relatively few individuals from a specific sex-age component of the population (i.e. subadult males). Non-selective control of seal numbers may therefore not have the desired effect of reducing predation on seabirds, especially as indiscriminate culling may not even remove the problem animals (Lavigne 2003) and predation can potentially proliferate regardless of the general trend in seal population numbers. The practice of removing "problem" seals, as promoted in David *et al.* (2003) is probably a more effective method of dealing with seal-seabird predation – as was the case with the removal of one problem seal at Ichaboe Island in the 1990s and shown in specific cases of seal-fishery operational interactions elsewhere (Lavigne 2003). This measure was espoused in South Africa's recently promulgated Policy on the Management of Seals, Seabirds and Shorebirds (SSSP) (DEAT 2007), which states that "In cases where seals have been confirmed as preying on seabirds of conservation concern, either on land or at sea, and where the level of this predation is believed to pose a threat to the population status of the bird species or colony concerned, attempts should be made to identify and to cull the specific seals responsible for the predation". Because culled individuals may be replaced by others, such culling programmes require constant vigilance and continued effort to reduce or eliminate an interaction type (Lavigne 2003).

There have, however, been several calls made to go beyond merely culling problem seals, and to reduce or remove populations close to seabird colonies. For example, the CAMP report proposes "the control of numbers and distribution of seals, where they influence threatened seabirds" (du Toit *et al.* 2003), and Lambert's Bay locals dependent on the tourism industry have called for seal numbers to be reduced to save the gannet colony (Gosling 2006). Kemper (2006) suggests that displacing seal populations from North Reef and Little Ichaboe Island, which pose predation threats to penguin colonies at Possession and Ichaboe Islands, respectively, may have positive implications for penguin conservation. It is to be expected that such actions would have tangible effects from the point of view of reducing seal-seabird interactions. However, any decisions to exterminate, reduce or displace seal breeding colonies, whether through culling, deliberate disturbance or both, should not to be taken without careful consideration – especially where there is no guarantee that the actions will reverse declining seabird numbers at a given location. Reasons include ethical considerations and the potential for "knock-on" effects following disturbance at a breeding colony. According to Crawford *et al.*

(1989), the re-colonisation of an island by seals normally commences when non-breeding individuals haul out on the island near the water's edge. If further settling is undesirable, seals can be discouraged at this stage without inflicting injury or mortality, by a human presence. However, displacing or reducing a breeding colony once it has formed is a different matter. Considering the annual cycle of the Cape fur seal (David 1989), prolonged disturbance to a breeding colony at any time of the year, with the possible exceptions of late September and October months (at which time most pups have been weaned and the colony is relatively empty before the onset of the next pupping and mating season; David 1989), can disrupt nursing and result in death through starvation of pups. Stress may also cause females to abort their foetuses. The earlier in the pup nursing period that disturbance occurs the more severe will be the effects in terms of mortality. The chasing of pregnant females off Seal Island in False Bay during the 1987 pupping and mating season (the infamous "seal shooing" experiment), resulted in the mainland beaches in the vicinity of the island becoming littered with dead newborn pups, resulting in an outcry at the cruelty of the program (Wickens 1994).

Effects of the past seal disturbance programs at Mercury Island (DEAT 1993) and at Bird Island, Lambert's Bay (Oosthuizen and David 1988), in terms of seal mortality or failed pregnancies, were not monitored. It was only documented that seals from Mercury Island re-located to a site on the mainland (Dolphin Head) which subsequently became a breeding colony (MA Meÿer pers. comm.), and Oosthuizen and David (1988) proposed that it may have been breeding-age seals displaced from Lambert's Bay which established the breeding colony at Paternoster Rocks to the south. The latter subsequently became a crowded breeding colony which may serve as a source for seals which currently pose a predation threat to seabirds breeding at the islands in or near Saldanha Bay. The consequences for seabirds of the mass dispersal of seals to Mercury Island following sealing disturbance to the Wolf Bay and Atlas Bay colonies in Namibia, has already been discussed. According to anecdotes, the breeding colonies at Wolf Bay and Atlas Bay were themselves kick started by excessive summer sealing at the adjacent Long Islands (PB Best pers. comm.). Such situations were therefore examples of unintended knock-on effects that may result from intensive disturbance to a seal colony.

When Europeans first explored the islands off South Africa and Namibia, seals and seabirds co-existed on many of them (Shaughnessy 1984); seal-seabird predation was therefore probably a common feature before the advent of large-scale sealing and other modifications to the islands. The argument that seal-seabird predation can no longer be viewed as a "natural process" because humans have "…disrupted the natural functioning of marine ecosystems, e.g. by providing additional habitat for some species to breed, through decreasing the food of some species and through climate change…" (DEAT 2007) seems incongruous when one considers many of the other processes that currently impact directly and indirectly on the dynamics of the affected seabird populations. As discussed earlier, these include predation by "human-subsidised" bird populations such as kelp gulls (and also great white pelicans – de Machado 2007), fishery-related mortality, food shortages due to effects of fishing or environmental variability, oil spills and other pollution, avian cholera and other diseases which may be transmitted from domestic poultry, predation by terrestrial predators that include feral species, human disturbance and habitat destruction, including reduced breeding success due to the removal of guano and nesting material. However, while there is obviously no dearth of "artificial" causes of seabird mortality to focus conservation efforts on, seal-seabird predation was considered by some as the factor which can most amenably be counteracted by management intervention (Ward and Williams 2004). This may be attributable to seals being highly conspicuous, easily accessible and relatively easy targets.

Generally where the conservation status of one or more seabird species is threatened directly by another species (excluding humans), it is an introduced species that poses the problem and not an indigenous species (Burger and Gochfeld 1994). An exception was the predation and displacement of macaroni penguins (classified as Vulnerable, Anon. 2008) by the rapidly increasing population of Antarctic fur seals at Bouvetøya in the southern Atlantic (Isaksen *et al.* 2000, Keith and Harck 2001). Other examples include the predation of the threatened yellow-eyed penguin *Megadyptes antipodes* and southern royal albatross *Diomedea epomophora* by another threatened species, the New Zealand sea lion *Phocarctos hookeri*, which, like the Cape fur seal, is re-colonising parts of its previous range (Lalas *et al.* 2007, Moore *et al.* 2008). Any management solution involving the reduction in numbers, removal or range restriction of a naturally occurring species for the conservation of another (or others) is a complex issue, for which there are troublesome ecological and ethical considerations. In this, the question of how to manage the Cape fur seal population may be compared to the debate of how expanding African elephant *Loxodonta africana* populations in South Africa should be managed. Here, one school of thought advocates the culling of elephants under the precautionary principle, in favour of avoiding loss of biodiversity (Anon. 2006, Owen-Smith *et al.* 2006). Another group maintains there is no compelling evidence to suggest that there is over-population of elephants or that culling will significantly reduce their impacts, and further, that culling elephants ignores the roles of other factors (e.g. other herbivores, climatic cycles) in ecosystem change (van Aarde and Jackson 2006). Each of these perspectives is applicable to the Cape fur seal management dilemma with regard to seal-seabird and also seal-fishery interactions (e.g. Butterworth *et al.* 1988, Butterworth 1992).

Ultimately, however, it may be fair to say that any similarities between seals and elephants ends at how they are perceived by the various stakeholders in their management. McCallum (2006) proposes that those who advocate culling of elephants and those who do not, have in common a respect (and even love) of the animal, and that even those directly involved in the decision making and the act of culling, do so only as a last resort. Such sentiments are not always shared by those who advocate the culling of the Cape fur seal, which is commonly referred to with terms such as “public enemy number one” (see David 1989) or a “scourge” (Ward and Williams 2004). Again, this may be attributable to the conspicuousness of the seals and certain of their behavioural tendencies, which are predisposed to invoke emotional responses from fishermen or seabird enthusiasts. These include the often wasteful nature of depredations by seals on fishery catches (Wickens *et al.* 1992a) and the perceived cruelty of many seal-seabird predation events (e.g. Ward and Williams 2004). Therefore, just as the impact of seals on fish resources tends to be over-stated by the fishing community due to the high profile of seals around fishing operations (David 1987), the behaviour of some seals in the vicinity of seabird breeding colonies may have a similar effect. In the past, this may have caused the role of seals in the plight of seabird populations to be over-emphasised, or at least prevented due recognition from being given to other potential causes of conservation stress in seabird colonies or populations, as has been underscored repeatedly in this review.

The need to conserve declining seabird populations in southern Africa is self-evident, especially considering the alterations to the ecosystem and the diverse threats they face. It is also unquestionable that seal-seabird interactions, including predation and displacement, can have a negative impact on locally breeding seabirds. However, it is also clear that the declines of seabird populations over the last 100 years were mainly the result of human interference (including over-fishing) and historical bad management practices, including guano and egg collection. Therefore, the contention that removing seals is the most amenable management tool to conserve breeding colonies of penguins and other seabird species is not enough as it does not take the bigger picture into account. Moreover, considering the intricacies of marine food webs (e.g. Yodzis 2001) and human induced alterations to the ecosystem, there can be no guarantees that local reductions in seal numbers will result in increases in seabird numbers, which may ultimately be controlled by fluctuations in food availability (Butterworth *et al.* 1988) or other factors.

With such uncertainty, it follows that management decisions made under the precautionary principle should aim to minimise the potential damage caused by being based on wrong assumptions. Methods that minimise death and harm to seals and seal colonies should therefore be seriously considered before indiscriminate actions, such as the destruction of a seal colony, are undertaken. For example, to prevent displacement of African penguins, which based on Table 1 is the species most severely affected by competition with seals for breeding space, emphasis could be placed on enhancing the penguin's breeding habitat rather than simply removing seals. In the last few years, artificial structures have been introduced at some penguin breeding locations, including Halifax Island (Figure 1) (Kemper 2007b) and Dyer Island (Underhill 2006), to provide protection from the elements and from aerial predators, and thus enhance breeding success. A few artificial pipes that were introduced on Seal Island in False Bay in 1991 have apparently been beneficial to the small penguin colony situated amidst a highly dense seal colony (Crawford *et al.* 1995a). Providing artificial structures at other islands where seals potentially affect the breeding success of penguins through interference would seem to be a sensible management tool to mitigate for these effects. Artificial nests at locations where penguins currently do not breed, such as Seal Island in Mossel Bay, could encourage breeding and assist with mitigating effects of the eastward shift in the distribution of their prey (pelagic fish) on the penguin population (Crawford *et al.* 2008c). At certain locations, such as the gannet colony at Bird Island in Lambert's Bay, it may even be possible to reduce encroachment of seals into seabird breeding habitat through the erection of artificial barriers, as suggested by Shaughnessy *et al.* (1982).

South Africa's Government Guano Island Administration invested a lot of effort in constructing barriers on many of the seabird islands, including Dassen, Malgas, Vondeling, Ichaboe, Sinclair and others, during the first half of the 20th century[8] (Shaughnessy 1984). Most of these barriers were built to prevent the sea from washing guano away or to concentrate penguins into smaller areas to facilitate the collection of eggs and guano (Shaughnessy 1984). With seabird populations declining in the region and management objectives having duly shifted away from

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[8] Eleven Namibian islands that were annexed by the British Government in the 19th century, including Ichaboe and Sinclair, were part of South Africa until they were transferred back to Namibia in 1994.

exploitation of seabird products, it may be time to invest in a similar effort, this time towards improving the survival and reproductive success of seabirds using artificial structures, rather than for profit. Given the considerable growth in tourism to seabird colonies in recent years (DEAT 2007), management actions that are conducive to preserving the integrity of seabird colonies are likely to translate to profit in the long term.

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Table 1 Summary of island locations in South Africa and Namibia (see Figure 1) where, based on the literature, Cape fur seals have had negative affects on seabird species through competition for space (C)[1], and predation (P)[2]. An asterisk denotes that the seabird species in question is now absent from the location.

Colony	African penguin	Cape gannet	Great white pelican	Bank cormorant	Cape cormorant	Crowned cormorant	Kelp gulls
Seal Is (Mossel Bay)	C*						
Quoin Rock	C*		C*				
Geyser Rock	CP*			C			
Dyer Is	P	P			P		P
Seal Is (False Bay)	C		C*	C	C		C*
Dassen Is	P						
Vondeling Is	C						
Malgas Is		P					
Jacob's Reef	C*						
Bird Is (Lambert's Bay)	CP	P		CP*	CP		P
Elephant Rock	C*						
Sinclair Is	C						
Pomona Is[3]							
Albatross Rock	C*						
Possession Is	P						
Long Is	C*						
Halifax Is	P						
Ichaboe Is	P	P		P	P	P	
Mercury Is[3]	C	C		C	C		
Hollams Bird Is	C	C*					

[1] Crawford *et al.* (1989, 1994, 1995a, 1999), du Toit *et al.* (2004b), Rand (1951, 1952b, 1963a), Shaughnessy (1980, 1984), Shaughnessy and Shaughnessy (1978), Shaughnessy *et al.* (1982), Williams and Dyer (1990), Williams *et al.* (2000), Wolfaardt and Williams (2006).

[2] Cooper (1974), Crawford and Cooper (1996), Crawford *et al.* (2001), David *et al.* (2003), Makhado *et al.* (2006), Marks *et al.* (1997), Navarro (2000), Rand (1959, 1967), Rebelo (1984), Shaughnessy (1978), du Toit *et al.* (2004a, 2004b), Ward and Williams (2004), Wolfaardt and Williams (2006)

[3] Predation incidents at Pomona and Mercury islands are also documented (Crawford and Robinson 1990), but which seabird species are involved is not specified.

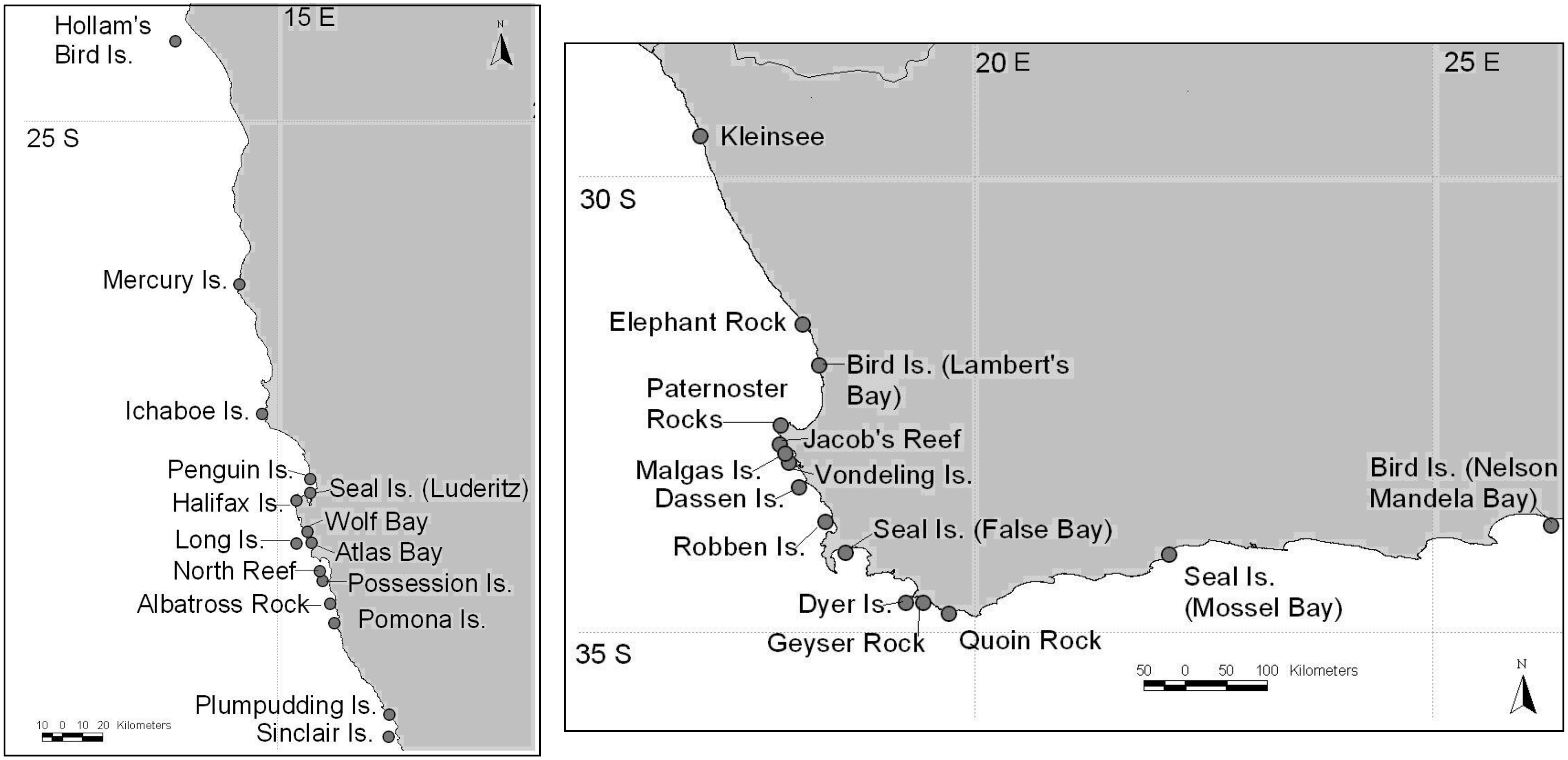

Figure 1 Maps of Namibia (left) and South Africa, indicating the locations of mainland Cape fur seal breeding colonies and islands mentioned in the text and in Table 1.

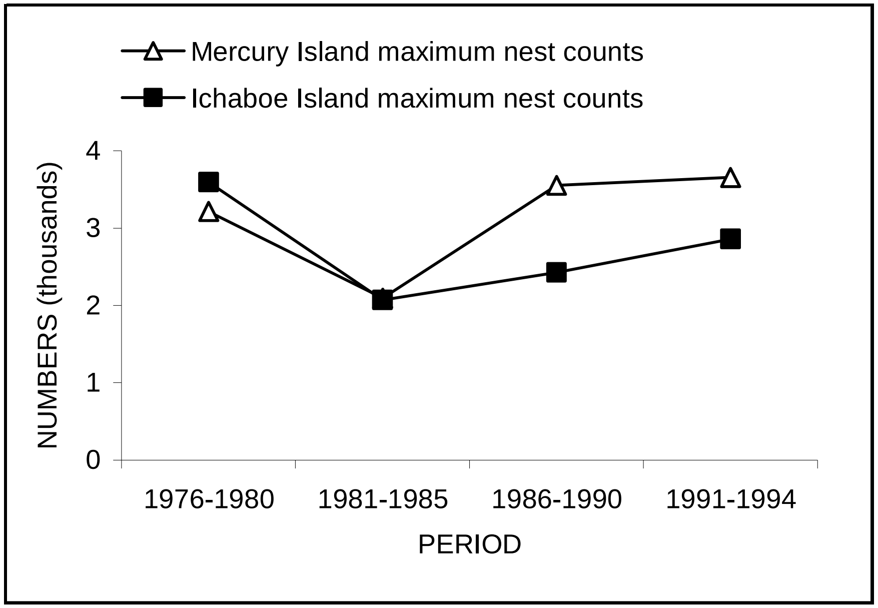

Figure 2 Trends in the maximum African penguin nest counts at Mercury and Ichaboe Islands in Namibia, during four periods between 1976 and 1994 (based on Table I of Crawford *et al.* 1995b).

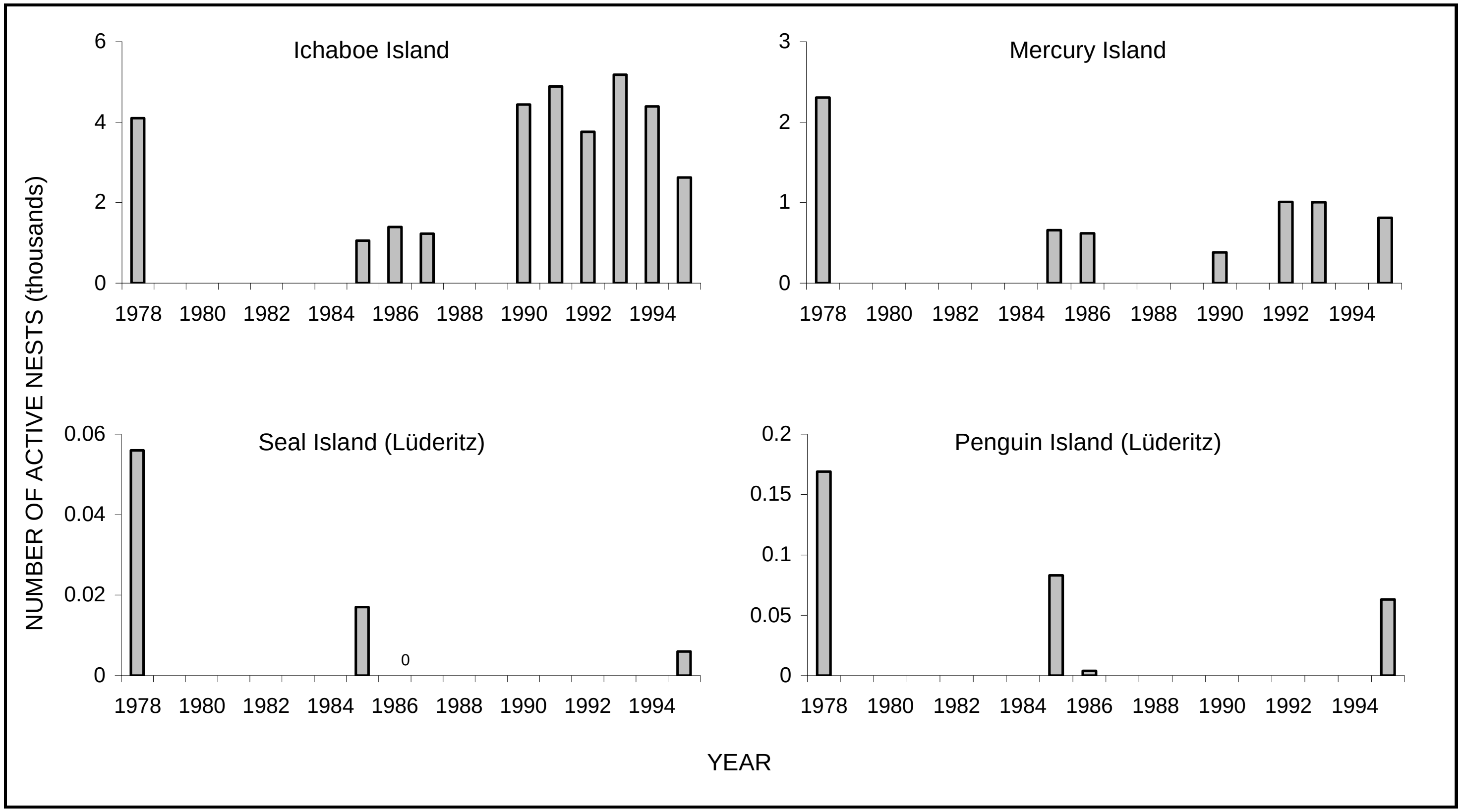

Figure 3 Counts of the maximum number of active bank cormorant nests at Mercury, Ichaboe, Seal and Penguin Islands in Namibia, between 1978 and 1995 (adapted from Figure 5 of Crawford *et al.* 1999). No bar indicates no count conducted, a 0 indicates a count of 0.

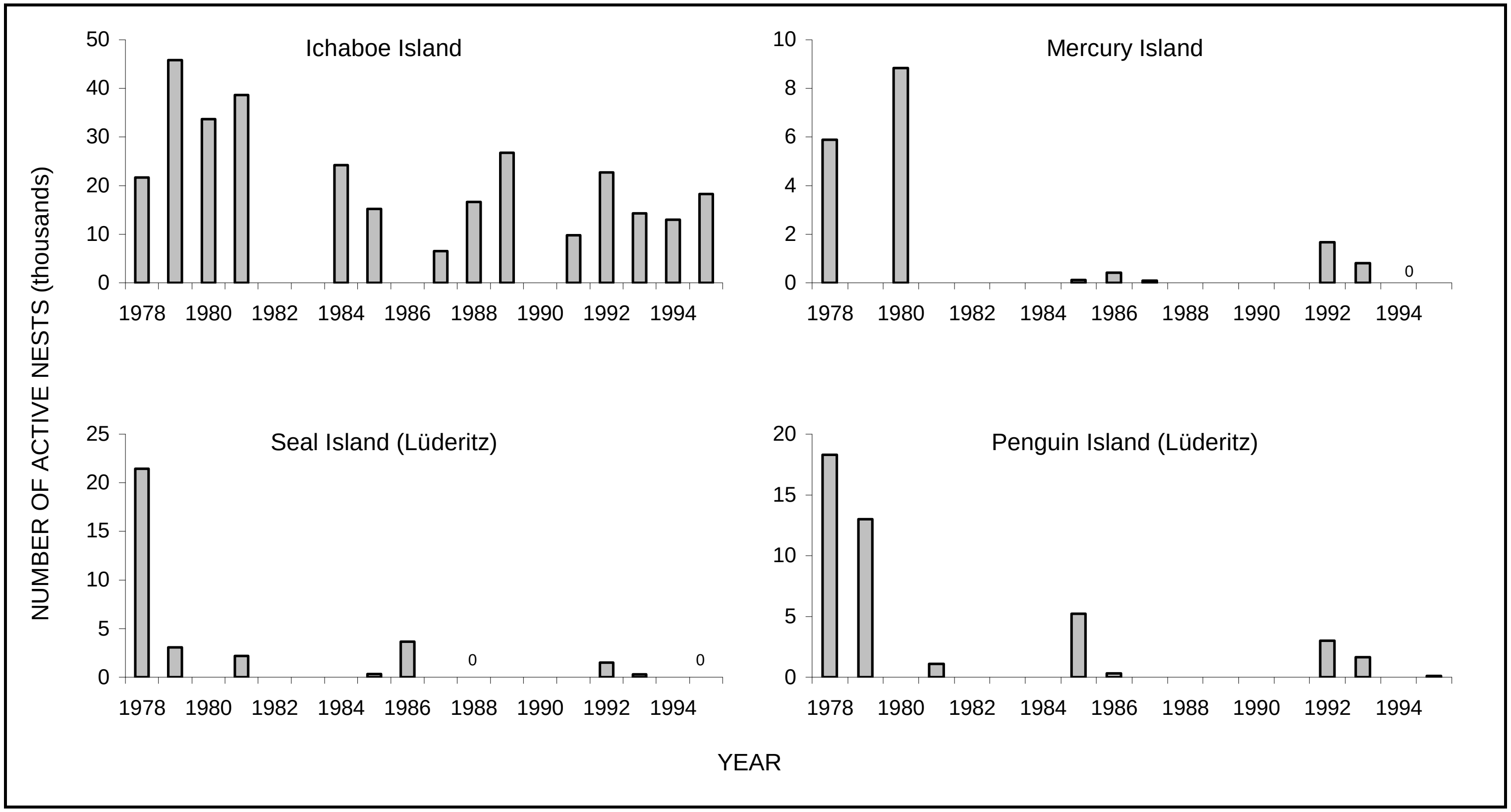

Figure 4 Counts of the number breeding Cape cormorant pairs at Mercury, Ichaboe, Seal and Penguin Islands in Namibia, between 1978 and 1995 (based on Table 1 of Crawford *et al.* 2007). No bar indicates no count conducted, a 0 indicates a count of 0.

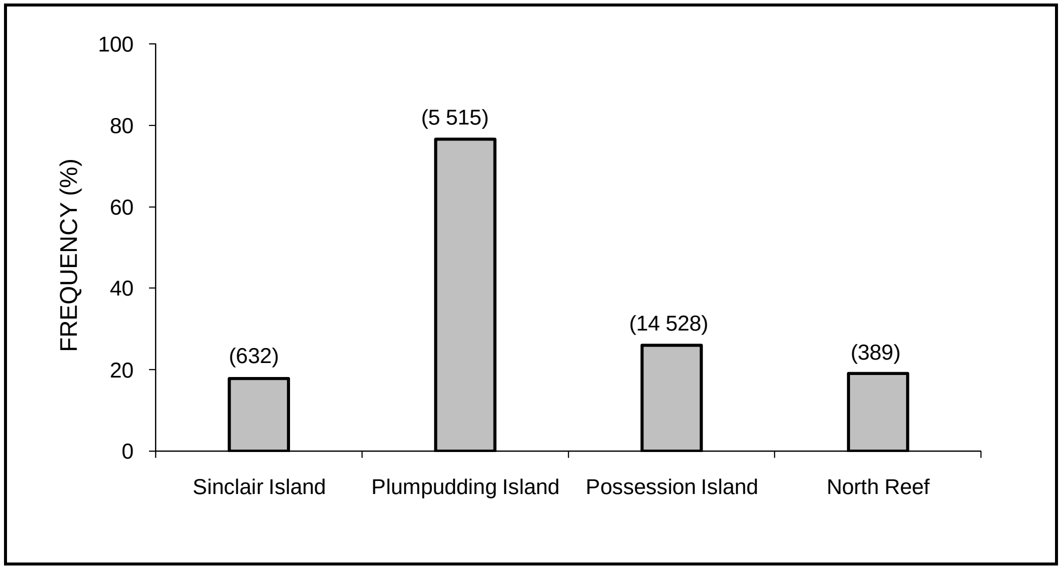

Figure 5 Counts of African penguins at Sinclair, Plumpudding and Possession Islands and North Reef in Namibia in 1967, shown as a percentage of the 1956 counts at the same colonies (taken from Table 1 of Shelton *et al.* 1984). The actual counts for 1967 are given in parentheses.

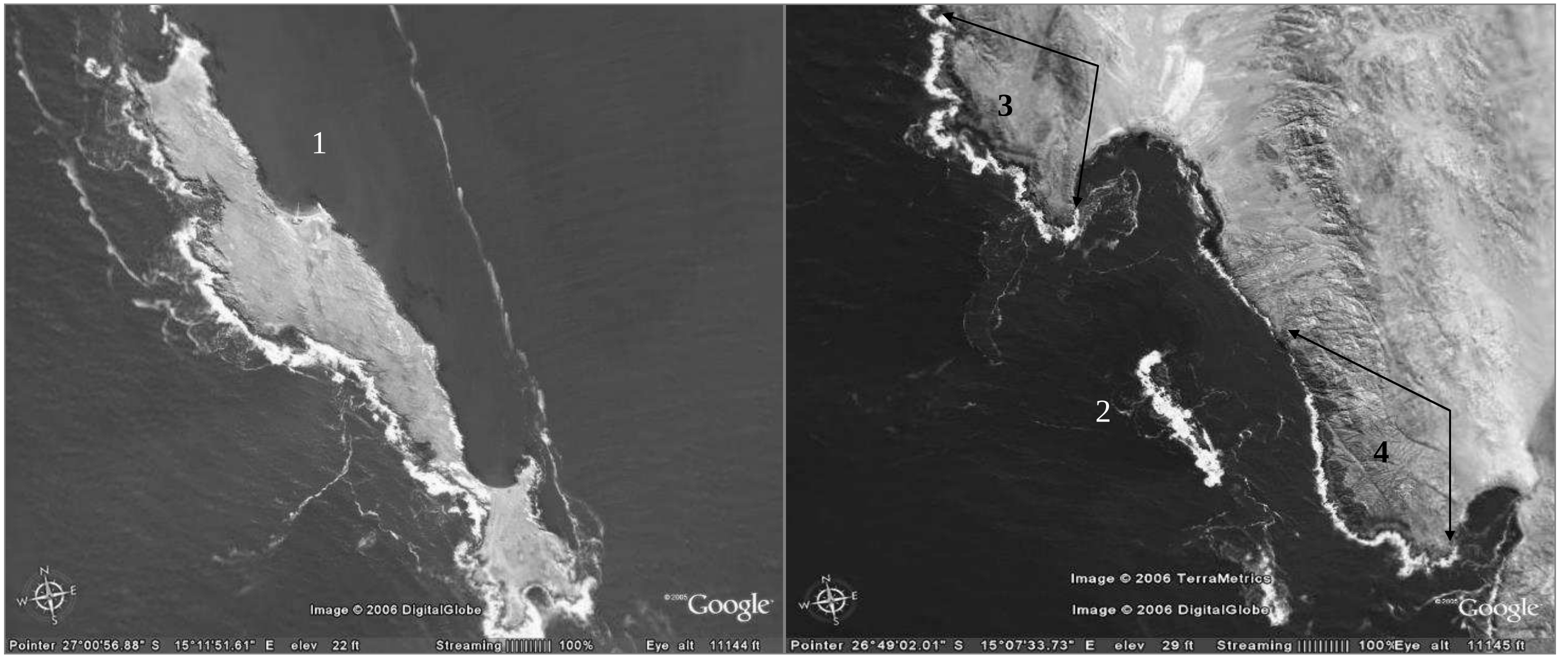

Figure 6 Google Earth images (http://earth.google.com/) of Possession Island (1), Long Islands (2), Wolf Bay (3) and Atlas Bay (4) Cape fur seal breeding colonies in Namibia. The latter two colonies are the darkened patches on the mainland between the two sets of arrow-heads. The two images are pictured at approximately the same scale (eye altitude c. 3 400 m).

CHAPTER 4

Spatio-temporal effects of research-related disturbance at a Cape fur seal breeding colony

Abstract

Investigator disturbance can potentially threaten study populations, influence research findings and compromise the welfare of individual animals. In this study, experimental sites (subjected to intensive investigator disturbance) and control sites (stayed relatively disturbance-free) were demarcated on a time series of aerial census photographs of a Cape fur seal *Arctocephalus pusillus pusillus* colony in Namibia. Retrospective analysis of seal numbers before and after investigator disturbance at the two experimental-control site pairs showed significant reduction in the ratio of animals at experimental sites relative to the control sites during the time series. The pattern was consistent between separate counts that were conducted of both adult seals and pups. The most likely explanation for the observed changes in spatial structure was that animals dispersed from or avoided the experimental sites as a result of disturbance. Implications for the representativeness of data collected from disturbed experimental sites were discussed.

Keywords: Aerial census, *Arctocephalus pusillus pusillus*, breeding colony, breeding season, disturbance, investigator, Namibia, research

Introduction

Effects of human disturbance on marine animals, especially seabirds, cetaceans and seals, have increasingly become the subject of marine biological studies. Such research studies mostly consider the disturbance impacts of activities such as tourism, mineral prospecting and military operations on individuals, groups or populations of animals (e.g. Beale and Monaghan 2004, Boren *et al.* 2002, Fernandez-Juricic *et al.* 2005, van Polanen Petel *et al.* 2008). There have also been an increasing number of “self-directed” research studies, aimed at assessing effects of investigator disturbance on marine animals (e.g. Engelhard *et al.* 2001, 2002, de Villiers *et al.* 2006). While not all such studies have shown significant effects (e.g. Wilkinson and Bester 1988, McMahon *et al.* 2005), it is well known that disturbance from field research activities can negatively impact upon the welfare of study animals through causing physical injuries or distress (Gales *et al.* 2003). The accumulation of such effects could potentially have an impact upon the demographic factors of a study population such as survival and reproduction (Blackmer *et al.* 2004), which is a concern especially if the study population is under threat (Caughley and Gunn 1996). An additional concern that needs to be considered is the potential impact of investigator disturbance upon research findings (Caughley 1977, Rodway *et al.* 1996).

Many marine animals, such as seabirds and seals, congregate ashore in colonies during part of their life cycle, and are thus relatively accessible for research and monitoring studies (Montevecchi 1993, Kirkman 2007). Numerous investigations of demography, reproductive performance and behaviour of seals and seabirds have been conducted in order to monitor the conservation status of populations, provide indicators of alterations in trophic functioning and other ecosystem changes or, in the case of exploited populations, to determine harvesting levels (e.g. Wickens *et al.* 1992, Boyd and Murray 2001, Reid 2002, Diamond and Devlin 2003, Crawford *et al.* 2006). Although certain data measures may be obtained remotely (e.g. abundance from aerial censuses) others may require the physical capture and handling of individuals, for marking or sampling purposes (Hindell *et al.* 2003). Studies that require the capture and handling of animals and/or repeated intrusion into seal or seabird colonies can result in considerable disturbance, particularly during the breeding season when animals may be the most sensitive to the effects of disturbance (Boren *et al.* 2002).

The consequences of stress and disturbance caused to animals by investigators are often poorly understood, but in the context of seal or seabird colonies may include physiological effects of stress and exertion, deleterious effects on parent-offspring relationships (including abandonment of offspring) or displacement of animals from favoured areas (Gales *et al.*

2003). To be able to distinguish the effects of research-related disturbance on animals from other potential stressors, will require the comparison of study animals with a control set of animals. Ideally, variables used for comparison between study and control sets should be measured non-invasively or even remotely, so that the control animals remain undisturbed.

In this study, remote counts were used to retrospectively determine the effects of investigator disturbance at Atlas Bay, a large Cape fur seal *Arctocephalus pusillus pusillus* colony in Namibia. The counts were conducted using a time series of aerial photographs that were taken of the colony with the purpose of monitoring long term changes in the number of pups born there annually (see Chapter 2). The null hypothesis of the study was that disturbance caused by ground-based researchers at localised "experimental" sites within the colony over a period of the time series did not have a significant impact on seal numbers in such sites. This was tested by comparison of numerical patterns in seal numbers between the experimental sites and control sites.

Methods

The breeding season of the Cape fur seal

The timing of the Cape fur seal breeding season is consistently between late-October and early-January each year (David 1987). The breeding system is polygynous and is characterised by aggressive territorial breeding males, which defend harems of between 10 and 30 females for six or more weeks (Rand 1955, David 1987, Wickens and York 1997). Females give birth (almost always to a single pup) soon after hauling out on land in the breeding season, with most births occurring in a synchronised two week period in the first half of December (Shaughnessy and Best 1975, David 1987). Mating takes place soon afterwards, impregnating females to give birth again a year later. After mating, females depart to sea for a foraging trip and from then until weaning (usually 8–11 months after birth) they alternate between foraging bouts at sea and periods of suckling ashore (David and Rand 1986, David 1987).

Aerial photographic censuses

Since 1971, frequent censuses of the Cape fur seal population have been conducted as part of research on management issues such as seal harvesting and seal-fishery interactions (Shaughnessy and Butterworth 1981, Butterworth *et al.* 1995). During the censuses, near vertical, serial overlapping photographs were taken from a fixed wing aircraft flying parallel flight paths (transects) over colonies at a height of c. 100 m. Flying at lower altitude is avoided to prevent disturbance to the colony (MA Meÿer pers. comm.). Flights took place between 16 and 24 December (near the end of the breeding season) each census year

(Chapter 2). Successful censuses of Atlas Bay were conducted during 15 years between 1971 and 2006. From the inception of this time series to 2003, monochrome film photographs were taken, whereas after 2004, only digital colour images were taken during censuses. In 2004, both modes were used.

The study colony

The Atlas Bay seal breeding colony (26°50’S, 15°08’ E) is situated on the coast of the “Sperrgebiet” area in the south of Namibia. It is currently one of the three largest Cape fur seal colonies with over 60 000 pups born there in some years (Chapter 2), and extends along a c. 2 km stretch of coastline.

Experimental and control sites

Ground-based research has been carried out by researchers of the Namibian Ministry of Fisheries and Marine Resources (MFMR) at the Atlas Bay seal colony since the mid-1980s. During the breeding season, research activities were generally concentrated at localised study sites that were selected as manageable, representative sub-units of the colony. Two study sites, (which shall hence be referred to as experimental sites) situated in the northern half of the colony were considered in this study. Experimental Site 1 (ES1) was used for research in 1998, 1999 and 2000, and Experimental Site 2 (ES2) in 2001 and 2003 (Figure 1). I selected two control sites (CS1 and CS2) close to the experimental sites; they were matched for area, distance from the sea and initial density of seals. Therefore it could be assumed that any environmental or biological variables or human activities other than research that could potentially influence the distribution of animals in the colony were the same within each site-pair. The control sites were subject to little or no research activity during the breeding season. The four sites were demarcated on aerial photographs. Each experimental site represented less than 5 % of the total area of the colony (see Figure 1) and less than 5 % of seal numbers in the colony (comparison of counts from this study with whole colony counts in Chapter 2).

Research activities

Between 15 November and 15 January, research effort in the experimental sites was intensive, with 2–3 researchers making daily 2–6 hour visits to the sites during this time period. Research activities were mainly focused on obtaining data for parameters considered in the setting of seal harvesting quotas or providing indicators of feeding conditions (Roux *et al.* 2002). These included birth weight, sex ratio at birth, pup survival and growth. To be able to monitor individual pups longitudinally, it was attempted to mark all the newly born pups in the experimental site with uniquely numbered plastic tags.

Cape fur seals typically flee from approaching humans throughout most of the year (David 1989). During the breeding season however, breeding animals tend to remain in their structured harem formations in the event of mild human disturbance (Rand 1967). Such behaviour assists ground-based research in breeding territories. Nevertheless, despite the fact that researchers worked cautiously, their presence and their activities during the breeding season did appear to disturb seals in the experimental sites. A brief anecdotal account of this disturbance, based on personal observations, is given below.

Tagging of each pup entailed penetration of the trailing edge of their fore-flipper, which generally invoked a pain reaction. Females usually responded nervously or aggressively when their pup was temporarily removed from them and handled, especially when the pup reacted with cries. Belligerence of territorial males was increased when researchers were present, and they frequently made mock or real charges at researchers. Movements of seals in response to activities of researchers, including rare attempts of females or non-territorial males to escape towards the sea, resulted in pique between animals which amplified the commotion that is characteristic of seal colonies during the breeding season.

Researchers were also present in the colony outside of the breeding season. In most years, longitudinal monitoring of pup survival and growth was continued in experimental sites for several months after 15 January. However, visits to the colony were less frequent (weekly or twice weekly), and activities were in general considerably less intrusive than during the breeding season. For example, re-sighting of marks was conducted remotely using spotting scopes or binoculars, and marked pups were only reweighed if they could be captured without undue disturbance. These activities were not limited to the experimental site as was the case in the breeding season; rather they were implemented in neighbouring areas as well (including the control sites) because with development the pups extend their range, venturing progressively further away from their birth site to other areas of the colony (pers. obs.).

In summary, whereas experimental sites were distinct from the control sites in terms of the level of intensive research activity to which they were continually subjected over a two-month period during the breeding season, there was less distinction during the rest of year. This was because research activities were less frequent or intensive during the rest of the year and were more evenly distributed between the experimental sites and neighbouring areas that included the control sites.

Other human disturbance in the colony

Human access to the Sperrgebiet was restricted. Besides researchers, only a seal harvesting concession and a small tourism venture regularly accessed the colony during the time period examined in this study. Tourism was restricted to the southern part of the colony well away from the experimental and control site areas, therefore it could not have affected ratios of animals between these sites. Seal harvesting took place on a large scale at Atlas Bay for up to four and a half months of the year, with the season closing on 15 November. Apart from removing more than a third of the pups in the colony each year, the harvesting operations cause considerable disturbance to the colony (Morton *et al*. 2007, Kirkman and Lavigne 2010). However, considering their close proximity with each other, it can be assumed that experimental and control sites would have been similarly affected by harvesting.

Analyses

For each site pair (experimental and control site), a census conducted before the year when research activities commenced in the experimental site, and as many subsequent censuses as were available, were considered in the comparison (Figures 2 and 3). Photographs taken of Atlas Bay during the census in 2003 were unavailable and could not be used. Also, parts of experimental or control sites were missing in aerial photographs of the 1997 and 2006 censuses. Consequently, the 1997 census of ES2 and the 2006 census of ES1 were not considered. The former was substituted with the 1995 census.

The counting procedure followed that in Chapter 2. For each census year, the seals in each of the four sites were counted by two counters. The arithmetic mean of the two counts was taken to be representative, but subject to an error rule stating that they had to be within 20 % of each other. Where the initial counts varied by more than 20 %, additional counts were conducted until two counts within the error limit of each other were obtained. Separate counts were conducted for pups and non-pups (adults) in each site. The former could be easily distinguished from the latter on the basis of size and colouration (Shaughnessy 1987). Chi-square (χ^2) tests (Zar 1984) were performed to test whether the observed distributions of counts between experimental and control sites over the time period corresponded with the distributions that would be expected if seal numbers were independent of disturbance levels.

Results

Experimental site ES1 and control site CS1

In 1997, the year before research commenced at ES1, there were 22.4 % and 27.8 % more pups and adults in ES1 than in CS1, respectively (Figure 2). By 2001, the year after research had ceased at this site, numbers of pups and adults in ES1 were 43.9 % and 37.1 % of the corresponding numbers in CS1, respectively. There appeared to be a relative recovery after a few years of research inactivity at ES1, with pup and adult counts at 74.9 % and 81.7 % of the corresponding CS1 numbers in 2005, respectively. For both pups and adults, the observed distributions of numbers between ES1 and CS1 differed significantly from the expected (disturbance does not have an effect on seal numbers at the experimental site) distribution (Pups: $\chi^2 = 102.0$, df = 3, $p < 0.001$; Adults: $\chi^2 = 82.1$, df = 3, $p < 0.001$).

Experimental site ES2 and control site CS2

In 1995, before research at ES2 was initiated, the number of pups and adults counted at this site were 79.0 % and 14.0 % higher than in CS2, respectively (Figure 3). In the 2001 census, soon after research activity was initiated in ES2, pup and adult numbers in ES2 were 73.6 % and 75.5.5 % of the corresponding numbers in CS2, respectively. These percentages were reduced to 9.3 % and 24.1 % during the three censuses that followed the cessation of research activity in this experimental site. For both pups and adults, the observed distributions of numbers between the experimental and control sites differed significantly from the expected (disturbance does not have an effect on seal numbers at the experimental site) distribution (Pups: $\chi^2 = 438.5$, df = 4, $p < 0.001$; Adults: $\chi^2 = 108.0$, df = 4, $p < 0.001$).

Discussion

This study made the assumption that any changes in the abundance of seals within each of the experimental-control site pairs, was attributable to differences in the level of investigator disturbance. The proximity of each control site to the corresponding experimental site (Figure 1) ensured that all conditions which conceivably could have affected comparative counts, besides the level of research-related disturbance, were similar and therefore controlled for.

The observed spatio-temporal trends of the counts can be summarised as follows: counts of seals declined at each of the two experimental sites, relative to their controls, once they had been used for research. At each experimental-control site pair, there was congruency in the pattern between adults and pups and in every case the differences in the temporal trends between the experimental and control sites was found to be significant. It would therefore seem that the null hypothesis – that investigator disturbance had no effect on the spatial distribution of seals in the colony – should be rejected.

The mechanism(s) whereby investigator disturbance was translated into reduced seal numbers at the experimental sites was unclear, but the following were considered to be plausible hypotheses: (1) Increased offspring mortality before the timing of the aerial census, leading to reduced counts (of pups and of adults because females that lost their pup would not be tied to the colony afterwards) in the same year; (2) Reduced mating success or fertility of breeding females, leading to reduced numbers of adult females arriving to give birth the following season; (3) Reduced likelihood of offspring that were born in the experimental sites returning there to breed as adults; (4) Re-location of animals that encountered research-related disturbance to other areas. It was not possible to test all these hypotheses due to the lack of relevant data. Rather, they were examined logically in the context of the results, supporting evidence and the biology of the species, with the aim of eliminating unrealistic hypotheses and uncovering the most plausible explanation.

For Hypothesis 1, investigator disturbance could have exacerbated pup mortality in several ways, such as causing pups to be trampled by excited adults, causing desertion of pups by their mothers, compromising nourishment of pups (e.g. due to increased vigilance by mothers and the interruption of suckling bouts), or causing stress-related immuno-suppression leading to disease (Mattlin 1978, Suryan and Harvey 1999, Engelhard *et al.* 2002, Frid and Dill 2002, Cyr and Romero 2009). Loss of their pups would most likely entail early departure of adult females from the breeding colony, so that numbers of both adults and pups would be reduced at the time of the census. Whether or not investigator disturbance influenced pup mortality levels significantly cannot be tested empirically because observed levels of mortality in experimental sites were not controlled for. However, in 2001, the only year in which both research activities in one of the experimental sites and a census occurred, mortality of new born pups in ES2 up to the time the aerial census was estimated at between 11 % and 21 % (MFMR unpubl. data). This appears to be well within the limits of natural variability considering that de Villiers and Roux (1992) estimated mortality of new born pups in the first month (up to early January) to be as high as 36 %, using a non-intrusive approach. Furthermore, observed mortality was far less than the magnitude required to cause the ten-fold decrease in pup numbers at ES2 in the first season of research (Figure 2: difference between 1995 and 2001 pup count ratios). It was therefore unlikely that pup mortality alone was an important cause of the observed count patterns.

Light can be shed on the possibility that investigator disturbance reduced the mating success or fertility of breeding females (Hypothesis 2) by referring to the outcome of a past attempt to deliberately reduce the mating success of seals at a breeding colony during the breeding season. In a programme sanctioned by the South African government, seals on Seal Island (34°08’S, 18°35’E) in False Bay were driven off the island during daylight hours by personnel throughout the 1986 breeding season, to prevent them from pupping and mating successfully (Wickens *et al.* 1991). The rationale behind this was to reduce the rate of growth of the local seal population in the interests of protecting fish stocks in the area. However, although many of the breeding females were prevented from pupping successfully that year, with many of them giving birth at bathing beaches in False Bay in the absence of suitable alternative breeding habitat (Wickens 1994), the pup count on the island the following year was the largest to date (Wickens *et al.* 1991, Chapter 2). The programme thus failed to reduce the mating success of the island population, suggesting that seals must have come ashore at night to mate while undisturbed, or mated in the water. The large number of pups produced also suggests that the reproductive physiology of adults was unimpaired by the stressor. Considering that deliberately high levels of disturbance throughout a breeding season failed to reduce reproductive rates during the Seal Island programme, it is unlikely that the comparatively benign disturbance caused by researchers at the Atlas Bay experimental sites would have succeeded in reducing reproductive rates.

A degree of natal site fidelity is generally assumed for pinnipeds (e.g. Bradshaw *et al.* 2000, Grandi *et al.* 2008), even though it has been demonstrated for few species (e.g. Ridgway and Robison 1985, Lunn and Boyd 1991, Baker *et al.* 1995, Hofmeyr 2000). Assuming that female Cape fur seal offspring do tend to return to give birth in close proximity to the location of their own birth, investigator disturbance could have caused a reduction in the numbers of females born in the experimental site that returned as adults to give birth (Hypothesis 3). This could occur in two ways, firstly by significantly decreasing the survival rates of offspring, and secondly by reducing their attachment to the site through negative associations with disturbance. While either was possible in theory, such an effect would be lagged by at least three years from the first year of research disturbance because the age at first breeding in Cape fur seal females is 3–5 years (Wickens and York 1997). However, the 2001 census showed that effects of investigator disturbance on numbers of seals at ES2 were evident during the first season that the experimental site was in use (Figure 3). On the day of an aerial census, researchers did not enter the colony until the census was completed to avoid influencing the numbers and distribution of animals at the time of the fly-past, through disturbance. Therefore, it appears that the decrease in relative numbers at ES2 in 2001 (including a 10-fold decrease in relative pup numbers), in relation to the previous census, can only have been affected by research activity from mid-November up until the day before the census date. This indicates that at least a proportion of animals dispersed from (or avoided) the experimental site in the same season that it was in use, and that Hypothesis 4 apparently played a prominent role in the observed changes in count ratios.

Wild animals are generally thought to respond negatively to human disturbance because they associate it with predation risk (Frid and Dill 2002, Beale and Monaghan 2004). This was of particular relevance to the Atlas Bay seal colony considering that it was subjected to harvesting for up to four and a half months of the year during the study period. Gentry (1998) demonstrated that whereas adult female northern fur seals show fidelity to breeding sites, they are flexible enough to re-locate under unusual conditions such as when disturbance occurs. Dispersal of animals away from the disturbed breeding site (or avoidance of the disturbed site) was in line with the expectation, based on predation risk theory, that intense disturbance stimuli for prolonged periods causes habitat shifts (Frid and Dill 2002), in this case of breeding habitat. Furthermore, dispersing animals, especially females soon to give birth or females with young pups, would have experienced least cost if they did not move far from the disturbed site. Some animals may therefore have moved into the neighbouring control sites, consequently exacerbating the differences within experimental-control site pairs during and after periods of research activity in the experimental sites. Pups that re-located with their mothers would be expected to form an attachment to their new location, because Gentry (1998) demonstrated that suckling experience may be more important in a fur seal pup's initial attachment to a site than having been born there.

Fidelity of animals (including adults) to new areas (or continued avoidance of the experimental site) was the most likely explanation for the low ratio of animals between experimental and control sites for several years after research activities were terminated at the experimental sites (Figures 2 and 3). Nevertheless, at least at ES1, there appeared to be gradual recovery of numbers in the experimental site relative to the control site, a few years after research activities ceased (Figure 3). No such recovery was evident at ES2 but fewer years of census data following the termination of research activity were available for this site. This recovery at ES1 may be attributable to females which had not previously encountered investigator disturbance at the experimental sites, arriving there to give birth for the first time after the cessation of research activities at the sites. Eventual recovery of numbers at the experimental sites was consistent with the prediction that wild animals will access resources (in this case breeding space) in habitats previously affected by disturbance stimuli, once those stimuli are removed (Frid and Dill 2002). Effects of research-related disturbance on structure of the colony were therefore not expected to be permanent, at least with regard to the scale and duration of disturbance in this study. Considering this and the small proportion of the colony represented by each experimental site (see Methods), investigator disturbance during the breeding season of the scale reported in this study was expected to have a negligible impact on the integrity of the colony as a whole in the long term.

Dispersal of animals from the experimental sites can be seen as a behavioural response to a stress which can be defined as chronic (Cyr and Romero 2009), given its nature, duration and frequency (see Methods). Study animals which alleviate stress by dispersing and are lost to the monitoring study do not only reduce sample sizes and necessitate eventual enlargement of the experimental site or relocation of research to a new site, but also may have consequences for monitoring outcomes if the group composition of animals remaining at the experimental site is biased. For example, if significant numbers of females that originally bred there had dispersed on account of this effect, group composition of breeding females, after one or more seasons of research at a site, may be biased towards first-time breeders which had not been exposed to investigator disturbance at the site. In studies elsewhere, young, inexperienced fur seal mothers have been associated with pups that were smaller at birth and have lower growth and survival rates than the pups of older, more experienced females (Lunn *et al.* 1994, Georges and Guinet 2001). This bias could have implications for the representativeness of monitoring samples at Atlas Bay. While this is speculative until proven empirically, the reasoning is sound and for future monitoring of this nature it may be advisable to annually rotate sites that are the focus of intensive research, perhaps by using each site no more than once per generation length of the study animal, although the possibility of between-site effects may need to be examined.

Conclusions

By investigating spatio-temporal patterns in numbers of animals within a large seal colony over periods of time, it was possible to show an effect of investigator disturbance on the structure of the seal colony, an effect that can be reasonably assumed was symptomatic of stress caused by research activities. Through a process of deduction, dispersal of animals from the disturbed sites was determined to be the most plausible mechanism whereby disturbance could be translated into decreasing ratios of seal numbers between experimental and control sites. Author's of previous papers have partly attributed breeding dispersal of Cape fur seals and the development of new breeding colonies during the population's recovery from past over-exploitation to human disturbance related to seal harvesting or management interventions (Rand 1972, Oosthuizen and David 1988, Crawford *et al.* 1989, Wickens *et al.* 1991). However, the links between disturbance and breeding dispersal have generally been anecdotal or speculative, and evidence that other factors such as resource limitation or prey shifts did not influence the dispersal of breeding animals, have been lacking. The results of this retrospective study support the hypothesis that human disturbance is associated with dispersal of seals. Other hypotheses that were taken into account included effects of disturbance on survival or philopatry of pups born in the experimental sites, or on the mating success of adults. These theories were considered to be less important or negligible after examining them in the context of the available evidence and the biology of the species. However, their importance may increase under disturbance regimes of different severity and extent. Empirically testing the hypotheses put forward in this study presents opportunities for further research; for example, assessing movements between disturbed and control sites or comparing pup mortality between such sites. However, avoiding a potentially confounding effect of investigator disturbance in control sites would pose a considerable challenge for these types of studies.

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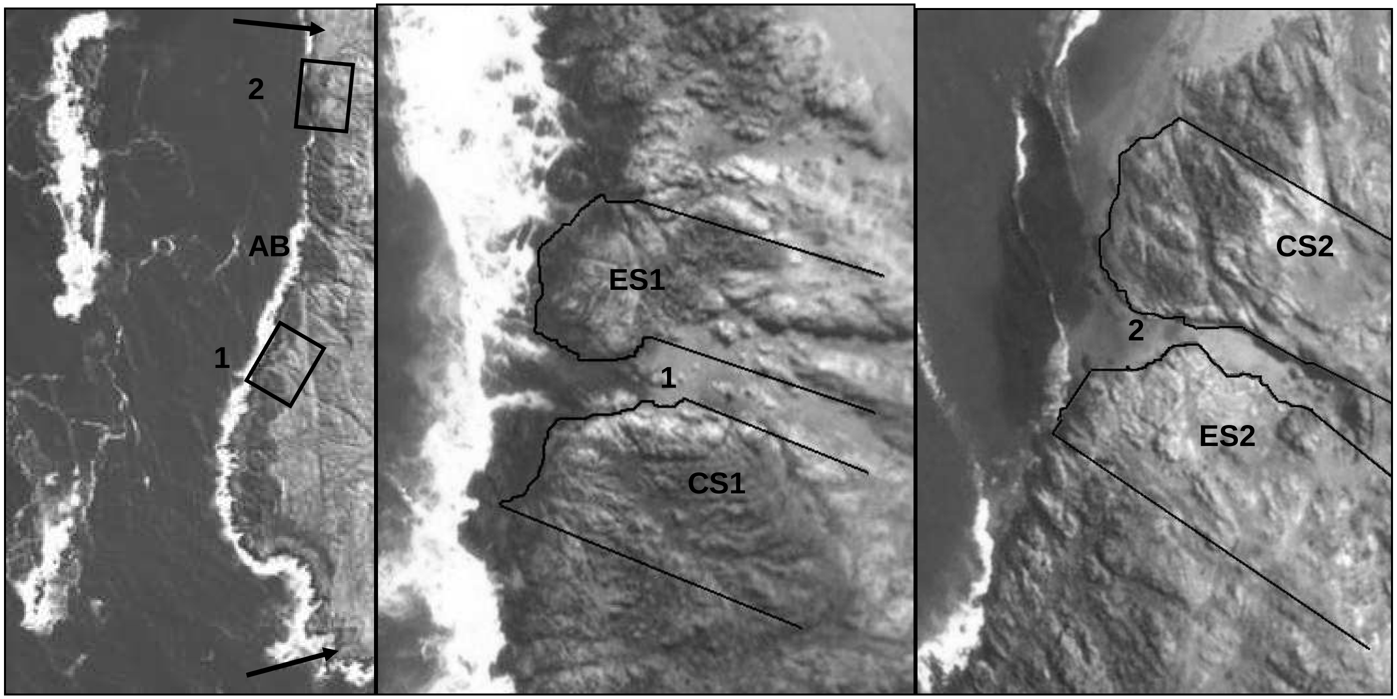

Figure 1 Google Earth images (http://earth.google.com) showing the situation of the Atlas Bay (AB) Cape fur seal breeding colony (the darkened section of the coastline between the arrows) in Namibia, including the locations of the first and second experimental-control site pairs, with the experimental (ES1 and ES2) and control (CS1 and CS2) sites enlarged in the second and third images. Long Islands are shown to the left of the Atlas Bay seal colony in the first image. The first image is at c. 2880 m altitude and the other two images at c. 290 m altitude.

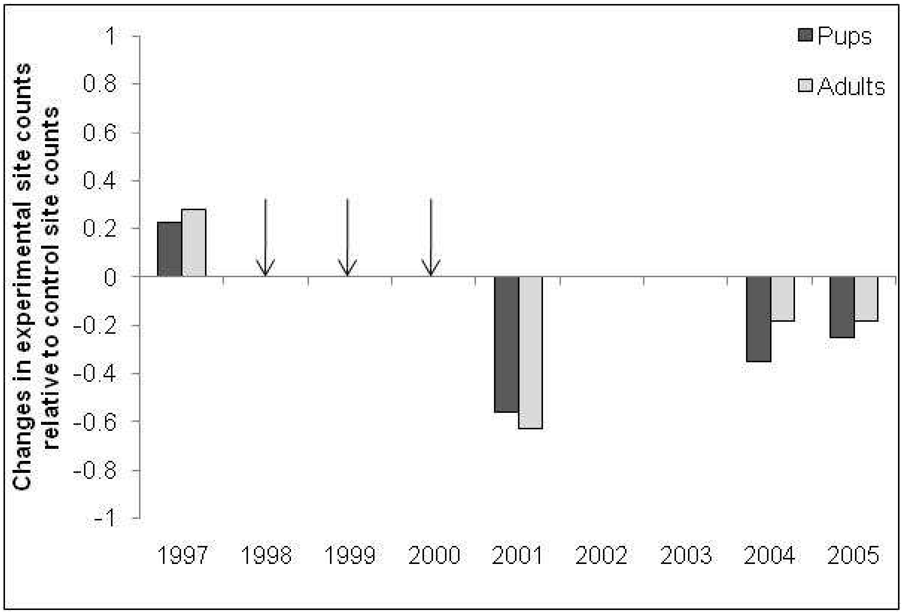

Figure 2 The ratios of Cape fur seals counted in the ES1 experimental site to those counted in the CS1 control site, on aerial photographs taken during censuses of Atlas Bay (Namibia) between the 1997 and the 2005 breeding seasons. Years during which research activities were conducted in the experimental site are shown with arrows.

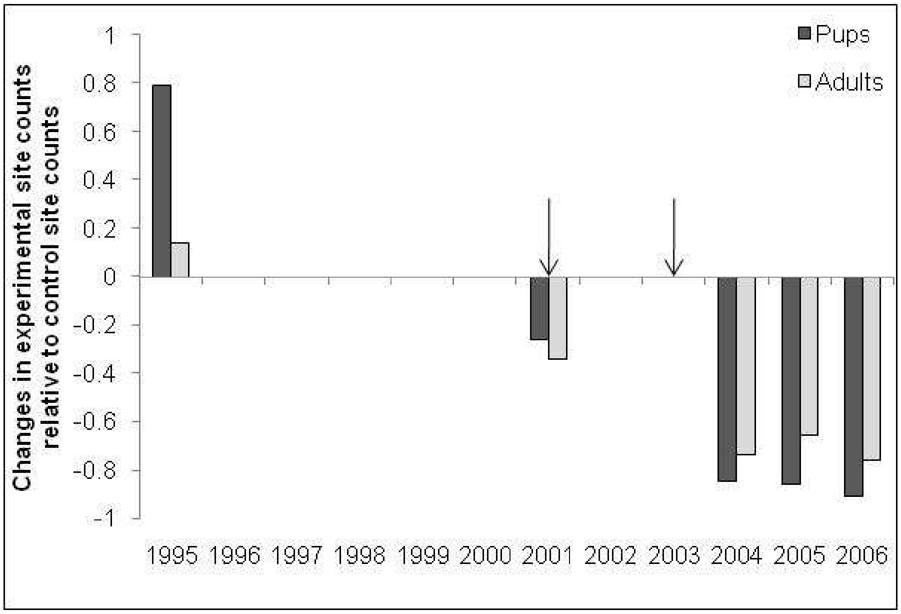

Figure 3 The ratios of Cape fur seals counted in the ES2 experimental site to those counted in the CS2 control site, on aerial photographs taken during censuses of Atlas Bay (Namibia) between the 1995 and the 2006 breeding seasons. Research activities were conducted in the experimental site in 2001 and 2003. Years during which research activities were conducted in the experimental site are shown with arrows.

CHAPTER 5

Do inter-colony differences in Cape fur seal foraging behaviour reflect large-scale changes in the northern Benguela Current Ecosystem?

Abstract

The northern Benguela Current Ecosystem adjoining Namibia has undergone considerable changes in recent decades, with reductions and northward shifts of key prey species that have had severe implications for marine top predator populations. The impact of such environmental variability on the foraging behaviour of the Cape fur seal *Arctocephalus pusillus pusillus* was assessed using satellite telemetry on animals in northern, central and southern Namibia. It was expected that seal foraging behaviour would reflect a gradient of deteriorating feeding conditions from north to south. Results showed that foraging trips were shorter in the central region, where seals fed over the continental shelf, than in the north or south, where seals fed at the shelf edge. However, whereas seals in the north showed strong fidelity to the colony at which they were tagged and to persistent, clustered foraging areas, seals in the south showed weak fidelity both to the colony at which they were tagged and to foraging areas, which were scattered and variable. Seals in the south also tended to disperse northward to other colonies, while concurrently adapting their foraging behaviour to local conditions. Flexible use of foraging space and colonies during the study period (2002–2004) demonstrates that the Cape fur seal is adapted for environments that are variable in time and space.

Keywords: *Arctocephalus pusillus pusillus*, satellite telemetry, foraging ecology, behaviour, Namibia, Benguela, ecosystem changes, fidelity

Introduction

Pinnipeds that breed in colonies demonstrate fidelity to central places where they breed and give birth (Boyd *et al.* 1994, Robson *et al.* 2004) and often to foraging areas at sea (Stewart and DeLong 1995, Bonadonna *et al.* 2001, Bradshaw *et al.* 2004). Fidelity to sites that provide crucial resources such as breeding space or food is believed to confer advantages to animals (e.g. social stability or familiarity with local resources) and is expected to be most rewarding in predictable environments with a steady food supply (Greenwood 1980). However, in the event of environmental variability that diminishes the supply of a crucial resource, the flexibility to utilise alternative sites may be a key to the persistence of a population.

At least part of the range of the Cape fur seal *Arctocephalus pusillus pusillus*, an endemic to the southern African subregion, is considered to be a highly variable environment (van der Lingen *et al.* 2006). This refers to the northern Benguela Current Ecosystem, which is adjacent to the coastline of most of Namibia, from the Angola-Benguela front in the north to the Lüderitz upwelling cell in the south (Figure 1). In this region, stocks of teleost prey species have declined markedly in recent decades and at least since the early 1990s and the distribution of certain stocks have shifted northward (van der Lingen *et al.* 2006). These changes have had considerable effects on top predator populations. For example, there have been substantial declines in the populations of Cape gannet *Morus capensis* and African penguin *Spheniscus demersus* in southern Namibia (Crawford *et al.* 2007a, 2007b) and a northward shift in the distribution of the Cape fur seal breeding population in Namibia has been documented (Chapters 2 and 6). There was circumstantial evidence that northward movement by adult seals from southern Namibian colonies has contributed to the northward range extension of the seal population (Chapter 2). Due to the lack of any previous in-depth study of the foraging ecology of the seal population in the northern Benguela Current Ecosystem, there has been little opportunity to investigate before and after effects of the wide-scale environmental changes that have occurred in this system. However, the wide geographical distribution of seal breeding colonies in Namibia, especially following the recent northward extension of the population's range, entails that foraging ecology may be compared between seals from geographically distinct areas. Feeding conditions at these colonies can be inferred from numerical trends (assuming that the latter are contingent mainly on prey availability) supported by information on the distribution and abundance of prey stocks around the time of the study, thus allowing for comparisons of foraging behaviour by seals experiencing different feeding conditions.

Satellite tags were deployed on male and female Cape fur seals from three colonies located in southern, central and northern Namibia, during June–July of 2002 and 2004. The timing of deployment allowed for tracking of females before and after the weaning of pups, and for males up to and during the period when they begin to establish territories at breeding colonies. Based on numerical trends of seals reported in Chapter 2 and information presented in van der Lingen *et al*. (2006) on the distribution and abundance of their prey in the northern Benguela Current Ecosystem in the early 2000s, the suitability of feeding conditions were expected to deteriorate from north to south, which it was expected would be reflected in the foraging behaviour of seals. More specifically, the following was expected: (1) seals in the south would perform longer foraging trips than seals in the north due to increased search times; (2) seals in the north would be more likely to show site fidelity, regarding both their colony and where they foraged; (3) if they left their area, seals from the south would move northward, congruent with the recent distributional shifts in prey populations and in the seal breeding population; (4) seals would demonstrate greater fidelity and shorter foraging trips during periods when they were constrained by reproductive activities (e.g. breeding, lactation) than otherwise; and (5) foraging behaviour and site fidelity would be affected by sex and size of animals.

Methods

The study animal

Cape fur seals have a polygynous mating system, characterised by territorial aggression on the part of adult males. Breeding occurs at the same time every year, between late October and early January, with adult males arriving at the breeding colony in October to establish territories. When the pregnant females begin to arrive in late October–early November, the territorial males attempt to herd them into harems on their territories, which they aggressively defend for six or more weeks, during which time they do not feed (Rand 1955). The females give birth to a single pup (twin births are rare) soon after hauling out on land, with most births occurring by mid-December (Shaughnessy and Best 1975). After giving birth, females alternate between foraging at sea and suckling on shore until the pups are weaned about 8–11 months later (corresponding to around July–November). Diet studies have indicated that Cape fur seals are opportunistic, generalist feeders. Some 30 prey species have been identified in their diet, with teleost fish comprising the most important prey type and with cephalopods, crustaceans and occasionally seabirds also featuring (David 1987, Lipinski and David 1990, Mecenero *et al.* 2005, 2006).

Field methods

In 2002 and 2004, satellite-linked platform terminal transmitters (ST18 and ST20, Telonics, Mesa, USA; referred to hereafter as satellite tags) were attached to a total of 29 seals at the Atlas Bay (AB), Cape Cross (CC) and Cape Frio (CF) breeding colonies, situated in southern, central and northern Namibia respectively (Table 1, Figure 1). Sexually mature seals (i.e. females with pups and males with pronounced necks and manes) were caught using a hoop-net with a canvas tube (David *et al.* 1990). The captured seals were restrained to boards with straps and given a valium injection before a satellite tag was glued to the guard hairs on the upper back (Fedak *et al.* 1984). Total length (TL) was measured and monel-metal identification tags (National Band and Tag Co., USA) were inserted in the trailing edge of both fore-flippers. The entire process took 45–90 minutes, before the seals were released towards the sea. Throughout the process, the animals' breathing was closely monitored and their flippers were repeatedly flushed with sea water to prevent hyperthermia.

Data collection and analysis

The tags transmitted on 401.65 MHz to receivers operated by Service Argos on board polar orbiting satellites. On average, locations were received at 6 hourly intervals. Argos provides gross estimates of location accuracy, with location classes 0, 1, 2 and 3 corresponding to accuracies of > 1 000 m, ≤ 1 000 m, ≤ 350 m and ≤ 150 m, respectively. Although classes A and B provide valid locations no accuracy estimate was computed for these classes and class Z contained invalid locations. A total of 17 739 locations was received, of which a large proportion were associated with the less accurate location classes (1 % class Z, 21 % class B, 17 % class A, 31 % classes 0–1, 16 % = class 2, and 14 % = class 3), probably on account of the seals' diving behaviour. Unrealistic locations were removed, including class Z locations, locations situated at greater than a 90 km straight-line distance from the previous location and locations that would have required swimming speeds of > 5 m s^{-1} to reach from the previous location (McConnell *et al.* 1992). The "cleaned" dataset consisted of 13 530 locations (16 % = class B, 16 %= class A, 10 % = class 0, 22 % = class 1, 19 % = class 2 and 17 % = class 3), with a mean of 520 locations per animal (SD = 227). These data were projected to the Universal Transverse Mercator zone 33S to obtain metric coordinates.

The locations were mapped in Arcview GIS (Version 3.3, Environmental Systems Research Institute, Inc.) and assigned to land or sea. Foraging trips were identified as the periods at sea between start and end positions on land. The locations were overlaid with a 10 km * 10 km grid matrix, and for each foraging trip the time spent in each grid cell that was visited during the trip, was estimated, assuming straight-line movements and constant speed between consecutive locations. Six behavioural descriptors were estimated from the data: (1) Trip duration (T_{Trip}) = the length of time between leaving and returning to land; (2) Maximum time (T_{Max}) = maximum time spent in any one of the 10 km * 10 km cells during a trip, with the location of T_{Max} was taken as a proxy for the main foraging site; (3) Depth at T_{Max} ($T_{MaxDepth}$) = the depth at the midpoint of the T_{Max} cell; (4) Distance from start to end locations on land ($D_{Start\text{-}end}$) = the direct distance between start and end locations on land for each trip, providing a measure of inter-colony displacement; (5) Time on land (T_{Land}) = time between trips; and (6) Latitudinal displacement (L_{Dif}) = the direct distance between the colony from where a trip was commenced and the colony where the animal was tagged. All of these calculations were performed in R 2.4.0. (R Foundation for Statistical Computing).

All descriptors, except L_{Dif}, were incorporated in a Principal Component Analysis (PCA) to explore the relationships between them, using S-PLUS 2000. To further analyse effects of sex, TL, season and colony on inter-colony differences in movements, non-linear generalised additive mixed models (GAMM) (Wood 2006) were employed, using the mgcv package in R 2.4.0. GAMM, which uses smoothing splines to fit non-linear functions of the predictor variables, allowed modelling of autocorrelation in the residuals of the observations of each individual, by defining individuals as random factors and defining the autocorrelation structure of the variance-covariance matrix. To identify the best matrix structure a full model (see below) with compound symmetry and first order autoregressive structures was used, with the structure giving the lowest value of Akaike’s Information Criteria (AIC) chosen. The optimal degree of smoothing was defined by generalised cross validation (Wood 2006).

Due to differences in reproductive constraints between sexes and over time, males and females were expected to have differing, non-linear responses with regard to season. A linear effect of TL and additive effects of sex and colony were also expected. The low number of tagged individuals prevented investigation of the effects of sampling year and interactions between sex and colony, so the 2002 and 2004 data were pooled. The full model was defined as

$$\log(Y) \sim \text{colony} + \text{sex} * \text{TL} + s(\text{date by females}) + s(\text{date by males})$$

where Y is the behavioural descriptor and s is the smoothing spline function.

This model was fitted separately for each behaviour descriptor except for L_{Dif}, which was defined by

$$\log(Y) \sim \text{colony} + \text{sex} * \text{TL} + s(\text{date by colony AB}) + s(\text{date by colony CC}) + s(\text{date by colony CF})$$

This model emphasised geographic rather than sexual variation because of primary interest was whether the distances that seals dispersed from their tagging colony varied between the three tagging colonies.

Following Wood (2006), a combination of two approaches were used to identify the best models: (1) The effects of linear and categorical variables and their interactions were judged by p-values (significance level $\alpha = 0.05$) and removed in a backward selection procedure; (2) Three different models evaluating the effects of date were compared using AIC: (a) separate non-linear fits for each sex (or colony, in the case of L_{Dif}), (b) combined non-linear fits for both sexes (or all three colonies), and (c) a linear fit of date, if the estimated degrees of freedom of the non-linear fit approached 1 (i.e. < 2). The combined model selection approach was chosen to reduce the number of models to be evaluated (Wood 2006). The fit of the models were evaluated visually by inspecting the residuals.

Results

The transmitters were active for between 20 and 257 days (mean = 146 days). During the 2002 and 2004 study periods, 647 and 374 periods at sea were identified respectively, ranging between four hours and 40 days. Periods at sea of < 24 hours (256 in 2002 and 260 in 2004) were excluded from further analyses. These generally comprised short trips to sea (mean cumulative distance = 13 km) which were most likely undertaken for thermoregulation during shore visits (Rand 1967). Also excluded were all trips with < 3 locations at sea and in which the reception of locations terminated while the animal was still at sea (e.g. due to loss of the transmitter or expiration of the battery). In all, 351 foraging trips in 2002 and 94 in 2004 remained following data vetting. The distribution of foraging trips is shown in Figure 1.

Tagged seals generally remained within 150 km of the shoreline at bathymetric depths of < 200 m off central Namibia and < 500 m in the north and the south. The Cape Frio seals foraged over the continental shelf (< 200 m depth) and at the shelf break (200–500m depth), within 200 km of the colony. They showed high fidelity to their colony and to foraging areas, foraging predominantly to the north of the colony at the Angola-Benguela front, although one male and one female travelled southward before hauling out first at Cape Cross then at Atlas Bay. The Cape Cross seals ranged up to 300 km from their colony, foraging on the shelf and frequently hauling out at neighbouring colonies. These seals travelled both southward and northward of the colony, with only one of them returning constantly to Cape Cross while three others re-located to Cape Frio. The Atlas Bay seals ranged up to about 400 km from the colony. None of these seals continued to return to Atlas Bay for the entire period that they were tracked, with most making extensive use of haulout sites between Cape Cross and Atlas Bay where their range overlapped with the seals tagged at Cape Cross. One Atlas Bay male travelled north to central Angola, and one male traversed the Lüderitz upwelling cell before hauling out at the Kleinsee colony in South Africa.

The average T_{Trip} lasted 5.71 days (range 1.1–50.7) and covered 24.6 grid cells or 2 460 km^2 (range 200 km^2–301 100 km^2). Females and males generally overlapped at sea, with the exception of the shelf break to the west of the Lüderitz upwelling cell, which was used exclusively by males (Figure 1). Mean time on land between foraging trips was two days, ranging between 0 and 10 days (after the removal of three extended periods during which all locations occurred on land, indicating that the transmitters had been shed while the animals were ashore; see Figure 2).

PCA

Two first principal components (PCs) explained 42 % and 25 % of the variation in the PCA. PC1 was negatively associated with trip time (T_{Trip}), maximum foraging time (T_{Max}), depth at T_{Max} ($T_{MaxDepth}$) and time on shore (T_{Land}), thus contrasting shorter trips characterised by lower T_{Max} and $T_{MaxDepth}$ with longer trips characterised by greater T_{Max} and $T_{MaxDepth}$ (Table 2). The longer trips were also associated with longer time spent on shore. PC2 was positively associated with the distance from start to end locations on land ($D_{Start\text{-}end}$) and T_{Land}, but negatively with T_{Max} (Table 2). This indicated that less time was spent at T_{Max} during trips when seals re-located to another colony, but more time was spent ashore on arrival at the new colony, compared to trips when seals did not re-locate.

GAMMs

Because the seals visited several other colonies besides their tagging colony, the northern Benguela Current Ecosystem was partitioned into four zones, zones 1–4 from north to south, to further investigate geographic patterns in foraging behaviour (Figure 1). Zones 2 and 3 are referred to herein as the central zones and zones 1 and 4 as the north and south zones, respectively. Foraging areas in each of the four zones were frequented by tagged seals throughout the study period, with seals from Cape Cross and Atlas Bay frequently overlapping in zone 3 (Figures 1 and 2). In the GAMMs, geographic zone was included as an additive effect and foraging trips were assigned to the zone where the trip started. A better fit of the GAMMs was achieved using the first order autoregressive than compound symmetry in the variance-covariance structure (AIC = 528.31 vs. AIC = 531.88 respectively).

Trip time varied by geographic zone ($F_{3,414} = 17.4$, $p < 0.001$), colony ($F_{2,23} = 11.3$, $p < 0.001$), TL ($F_{1,23} = 146.8$, $p < 0.001$) and sex ($F_{1,23} = 79.6$, $p < 0.001$), with no interaction apparent between sex and TL ($F_{1,22} = 1.2$, $p = 0.27$). A model with non-linear effects of date fitted for the sexes combined (AIC = 534.12) had a marginally better fit than when the sexes were modelled separately (AIC = 534.40). The selected model accounted for 35 % of the variation (R^2). Trips initiated in zones 1 and 4 were longer than trips initiated in the central zones (Table 3). Also, Cape Frio seals generally undertook longer trips than seals from Atlas Bay and Cape Cross (Table 3). Trip time increased with increasing body size ($e^{0.033\pm0.003}$ days cm^{-1}), and females conducted longer trips than males (contrast between females and males = $e^{0.91\pm0.12}$). However, due to the larger size of males than females, the predicted T_{Trip} of males was generally longer than for females (Figure 3). Trip time increased from spring to summer then decreased again in autumn (Figure 3b).

The maximum foraging time (T_{max}) per trip was dependent on geographic zone ($F_{3,414} = 9.8$, $p < 0.001$) and TL ($F_{1,26} = 3.85$, $p = 0.05$), with the effects of colony and sex both insignificant ($p \geq 0.18$). Non-linear fits of date for both sexes combined provided a marginally better fit (AIC = 851.57) than for each sex separately (AIC = 851.60). The selected model accounted for 15 % of the total variance. Trip time was greater in zone 1 than zones 2, 3 or 4, and was positively related to TL ($e^{0.005\pm0.003}$ h cm^{-1}, Table 3). Seasonal changes in T_{Max} were similar for females and males, and followed the same patterns as for T_{Trip} (Figure 4).

Depth at T_{Max} was significantly influenced both by sex ($F_{1,25} = 4.60$, $p = 0.03$) and TL ($F_{1,25} = 8.96$, $p = 0.003$). The effect of date was best modelled as a linear effect combined for both sexes (AIC = 1 367.2) rather than a non-linear effect fitted for each sex separately, for the sexes combined or with linear interaction between sex and date (AIC ≥ 1 367.3). The selected model accounted for only 8.6 % of the variation. Depth at T_{Max} was greater for males (mean 125 ± 9 m) than for females (mean 95 ± 5 m), and was positively related to TL ($e^{0.05\pm0.02}$ m cm^{-1}) but negatively related to date ($e^{-0.001\pm0.0001}$ m day^{-1}).

The distance between start and end locations on land depended only on colony ($F_{2,25} = 4.67$, $p = 0.01$) and geographic zone ($F_{3,414} = 2.54$, $p = 0.05$). A model without any effect of date (AIC = 1 771.1) provided a better fit than models with linear or non-linear effects of date (AIC ≥ 1 772.7). The distance between start and end locations was greater for Atlas Bay seals than Cape Cross seals and smallest for Cape Frio seals (Table 3). Similarly for geographic zones, $D_{Start\text{-}end}$ was greater in zones 3 and 4 than in zones 1 and 2 (Table 3). The selected model accounted for 15 % of the variation.

Time on land was dependent on TL ($F_{1,25} = 35.27$, $p < 0.001$) and sex ($F_{1, 25} = 8.27$, $p = 0.004$) only (all other $p \geq 0.14$). As for $D_{Start\text{-}end}$, a model without any effect of date (AIC = 568.6) provided a better fit than models with linear or non-linear effects of date (AIC ≥ 570.6). Time on land increased with increasing TL (0.01±0.003 h cm^{-1}) and was slightly shorter for females (mean = 1.6 days, SE = 0.1) than males (mean = 1.7 ± 0.1 days). The selected model accounted for only 4.0 % of the variation in time spent on land. Of the 17 seals that were still carrying functioning transmitters by December, five females went ashore for an extended period, suggesting that they may have given birth (Figure 2). Four of these females went ashore at their tagging colony (Atlas Bay and Cape Cross), whereas one Cape Frio female went ashore at Atlas Bay. Two males also went ashore for extended periods: one Cape Cross seal in Cape Cross and one Atlas Bay seal in Conception Bay, north of Atlas Bay (Figure 1). However, extended periods on land were also observed throughout the study period, not only at the time of breeding (Figure 2), which may explain why no seasonal pattern in T_{Land} was evident in the GAMM (Figure 2).

Latitudinal displacement depended on TL ($F_{1,24} = 5.83$, $p = 0.016$) and colony ($F_{2,24} = 23.84$, $p < 0.001$) as main effects. A nonlinear fit of date by colony (AIC = 11 758.44) provided a better fit than non-linear or linear fits of all seals combined or in linear interaction with colony (AIC ≥ 11 758.65). Latitudinal displacement was independent of sex, both as a main effect and in interaction with TL (both $p > 0.10$) but decreased with increasing TL (est. -2.3 ± 1.0 km cm^{-1}). Latitudinal displacement remained close to zero for both Cape Cross and Cape Frio seals (Figure 5), but towards the start of the breeding season, one Cape Frio female moved southward to Atlas Bay, resulting in high negative values for the predicted values of the GAMM (Figure 5). By excluding this seal from the analysis, L_{Dif} Cape Frio seals remained close to zero throughout the study period (Figure 5). The selected model (including all individuals) accounted for 49 % of the variation in L_{Dif}.

Discussion

Geographic patterns in Cape fur seal foraging behaviour

Measures of foraging trip and shore visit duration were within the ranges of previous observations for Cape fur seals (Gamel *et al*. 2005) and other fur seals (Arnould and Hindell 2001, Robson *et al.* 2004, Staniland *et al.* 2004, Page *et al.* 2006). The distribution of locations for the tagged seals were generally confined to the shelf and shelf break, between the Lüderitz upwelling cell in the south and the Angola-Benguela front in the north (Figure 1). The coastal areas to the south of Cape Cross, which are characterised by oxygen deficient waters and low biological production (Chapman and Shannon 1987, Roux 2003), were avoided (Figure 1).

The duration of foraging trips by seals in the north and south (zones 1 and 4) were longer than in the central zones (2 and 3). Longer foraging trips may indicate increased travelling or search times relative to foraging times and hence an increased foraging cost (Boyd *et al.* 1994). The PCA indicated that longer foraging trips were followed by longer shore visits, suggesting that seals performing longer trips required additional time ashore to recover, or, in the case of adult females, to nourish their pups. The cost of the longer foraging trips may have been compensated for by an increased abundance of prey, considering that longer foraging trips were associated with increased foraging times (Table 2).

Although long foraging trips to the shelf break were characteristic of the animals under study from Cape Frio and Atlas Bay, there were important differences in foraging behaviour between seals from these two colonies. The maximum foraging time of Atlas Bay seals was shorter than for Cape Frio seals, indicating a smaller ratio between time spent foraging and time spent travelling or searching by Atlas Bay seals. The foraging areas visited by Atlas Bay seals were scattered and variable, in contrast to those to the north where they were aggregated and persistent (Figure 1). Furthermore, seals from Atlas Bay tended to re-locate to other colonies, a behavioural strategy that was associated with reduced foraging time according to the PCA results (Table 2). The duration of the foraging trips of seals in the central zones (2 and 3) region were shorter than those in zones 1 and 4, with foraging occurring over the shelf and not the shelf break. Although seals from Cape Cross frequently moved between colonies (Figure 1), the displacement trips were shorter than those of Atlas Bay seals. Whereas the Atlas Bay seals showed a net northward displacement during the study period, no net changes in latitude were observed for the Cape Cross and Cape Frio seals, with the exception of the single female that had moved from Cape Frio to Atlas Bay by the end of the study period.

Although this study provided no information of feeding success, it was hypothesised that geographic variation in foraging behaviour and site fidelity was attributable to geographic variation in local prey availability. The targeting of prey on the shelf in the central zones required shorter trips than the more distant prey along the shelf edge targeted by seals in zones 1 and 4. Furthermore, the long trips to persistent foraging areas in zone 1 appear to be relatively rewarding as the seals showed high fidelity both to their colony and the foraging areas throughout the study period. These foraging areas were located either to the north or south of the colony, coinciding with the position of the Angola-Benguela front and an upwelling cell in the vicinity of Cape Frio respectively, regions where potential prey such as horse mackerel *Trachurus trachurus capensis* and lantern fish *Lampanyctodes hectoris* are known to be abundant (Cruickshank 1983, Axelsen *et al.* 2004). In contrast, the long trips, low fidelity and northward net displacement of Atlas Bay seals probably reflects poor feeding conditions in the south. The main prey for Atlas Bay seals has been Cape hake *Merluccius* spp., gobies *Sufflogobius bibarbatus*, lantern fish and other small pelagic fish (Mecenero *et al.* 2006), but in the northern Benguela Current Ecosystem, the stocks of hake and small pelagics have declined in size and shifted northward in recent years (Cury and Shannon 2004, van der Lingen *et al.* 2006).

The large-scale commercial seal harvesting that takes place annually at Atlas Bay and Cape Cross between July and November (Morton *et al*. 2007) could also have had an impact on the behaviour of seals at these colonies. A large proportion of pups at these colonies are killed during the harvest. Not only does this remove the nursing constraints of many females, but considerable disturbance is caused at the colonies (Morton *et al*. 2007). Thus, the expected gradient in habitat quality may be partially confounded by harvesting, and the reduced fidelity to the Atlas Bay and Cape Cross may potentially have been influenced by the harvest. However, if seals from the disturbed colonies re-located to other locations on account of harvesting effects, they would be expected to settle at undisturbed colonies nearby, provided that feeding conditions in the area were good. Whereas Cape Cross seals that re-located did tend to move to colonies that were in relatively close vicinity (Figures 1 and 5), this was not the case for Atlas Bay seals, which generally undertook long distance northward displacement trips, despite the presence of several undisturbed colonies in zone 4 (including van Reenen Bay and others, Figure 1). The direction of displacement trips was congruent with the documented shifts in the distribution of prey in the region and of the seal population itself (van der Lingen *et al.* 2006, Chapter 2).

Seasonal, sexual and size-related variation in foraging behaviour

Both the trip duration and maximum time spent foraging by the study animals (both sexes) increased from June to August–September, before decreasing again ahead of the breeding season (Figures 3 and 4). Increases in foraging trip duration by adult females between giving birth and the end of lactation, and again after the end of lactation, have previously been observed in the Australian fur seal *Arctocephalus pusillus doriferus* (Arnould and Hindell 2001). The increase in trip duration of females up to August therefore suggests that the pups were weaned, or possibly lost to harvesting in the case of Atlas Bay and Cape Cross, before August. The reduced trip duration by males from October onwards was expected, because this is the period when males begin to congregate at colonies in preparation for breeding activity (Rand 1967, David and Rand 1986). However, the low trip duration of males in July was unexpected because at this time of the year males are not subject to reproductive constraints that would restrict their time at sea. It was possible that this behaviour was influenced by capture and deployment, which occurred in June–July; however, removal of the first post-tagging trip from the analyses did not alter the result. The cause of the short foraging trips by males at this time of the year thus remains uncertain.

Trip duration increased with body length for both females and males and males tended to forage in deeper areas and have longer shore visits than females. However, whereas strong inter-sexual competition or size-related ecological divergence have been indicated for some other fur seal species (Boyd *et al.* 1998, Page *et al.* 2005), extensive overlap in the at-sea distributions of the males and females under study suggest that such differentiation is lacking in the Cape fur seal. Larger seals of each sex did tend to forage at more distant and deeper waters than smaller animals, but this was probably related to the increased physical capabilities of larger seals.

The lack of any seasonal shift in the time on land between trips suggests that females compensate for changes in nutritional requirements by adjusting their time spent at sea, not on land. This pattern has also been demonstrated for Australian fur seals (Arnould and Hindell 2001). No significant increase in shore attendance time following the onset of the breeding season was recognised by the GAMMs, even though some seals spent long periods ashore in December (Figure 2). Cape fur seal females are known to spend between 3 and 9 days ashore following parturition and adult males may stay ashore for several weeks at a time (David and Rand 1986). However, substantial variability in shore attendance occurred throughout the study period (Figure 2), possibly reducing the ability to detect statistically significant changes in the duration of shore visits at the time of breeding.

Latitudinal displacement was found to decrease with increasing body length, which was consistent with the Baker *et al.* (1995) finding that colony fidelity increases with age until sexual maturity in polygynous seals. As the primary dispersing sex, generally, males tend to show less site fidelity than females (Greenwood 1980, Baker *et al.* 1995). In the animals under study, females moved frequently between colonies. However, the five females that were presumed to have given birth in December did so at their tagging colony, whereas another female dispersed from Cape Frio to Atlas Bay (Figure 2). Males also shifted between colonies, but because it was uncertain whether they had bred at their tagging colony the season before (unlike females with pups), it was uncertain whether they had actually shifted breeding colony between one breeding season and the next. Unfortunately, because most transmitters either stopped transmitting or were shed by the beginning of the next breeding season (Figure 2), the data were inadequate to thoroughly assess breeding dispersal. Nevertheless, the size-effect on latitudinal displacement suggests that among the sexually mature seals, younger seals were more prone to disperse than older seals.

The Cape fur seal – a flexible, generalist predator

Top predator populations in the northern Benguela Current Ecosystem have been exposed to severe environmental fluctuations and resulting food shortages, especially since the early 1990s. These events included an extended low oxygen episode affecting shelf waters off Namibia and a severe Benguela Niño that caused a warm water intrusion onto the Namibian shelf (Gammelsrød *et al.* 1998), causing declines of fish stocks as a result of mortality, poor recruitment and distributional shifts. With the distribution of certain fish stocks in the northern Benguela Current Ecosystem having shifted northward, prey resources for top predators off southern Namibia have remained depleted, despite reduced fishing pressure there since 2000 (van der Lingen *et al*. 2006). This has been interpreted as an indication of a ‘regime shift’ in the ecosystem, and it was considered unlikely that a recovery will occur within a short time period (Cury and Shannon 2004). The Cape fur seal population has to some degree been able to track the directional shifts in prey availability by successfully establishing new breeding colonies in central and northern Namibia, and its numbers have remained relatively stable (Chapter 2, Chapter 6). Other piscivorous predators, such as Cape gannets and African penguins, have been less robust to these changes and have declined by 70–90 % in Namibia over recent decades (Kemper 2006, Crawford *et al.* 2007a, 2007b).

This study shows that Cape fur seals undertook migrations between the time that pups were weaned (or lost to harvesting) and the commencement of the next breeding season, especially the seals from southern and central Namibia. The expectation that generalist predators such as seals should be flexible in their behavioural patterns (e.g. Staniland *et al.* 2004) was realised by the fact that tagging colony and geographic zone were the most important predictors of behavioural patterns in this study, and seals from one colony would alter their behaviour on entering a new zone. Flexibility in site fidelity and foraging behaviour in response to variable feeding conditions may demonstrate an adaptation to the dynamic environment of the Benguela Current Ecosystem, and precondition the seal population to persist at present levels despite adverse conditions in parts of its range. Nevertheless, five out of the six females under study that were presumed to have commenced breeding in December had returned to their tagging colonies, suggesting that fidelity to breeding colonies may counter dispersal as a behavioural response to environmental variability.

Most studies that have investigated fur seal responses to changing prey availability have focused on lactating females (e.g. Boyd *et al.* 1994, McCafferty *et al.* 1998, Lea *et al.* 2006) and have showed how they can adjust to forage optimally under changing conditions when restricted to operating at a local (colony) scale by reproductive constraints. This study focused mainly on a period when animals were not constrained by reproductive activities (i.e., between weaning of pups from one cohort and birth of pups of the following cohort) and thus was able to show evidence of flexible, regional-scale responses to environmental variability.

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Table 1 Details of the satellite tag deployments on Cape fur seals at three colonies in Namibia in 2002 and 2004.

Colony	Sampling dates	Number of individuals	Range of total length (cm)
Cape Cross	2–7 July 2002	6 females	137–184
		2 males	180–182
Atlas Bay	14–15 July 2002	5 females	136–142
		3 males	165–189
	20–21 July 2004	4 females	137–153
		3 males	159–193
Cape Frio	8 July 2002	3 females	139–150
		3 males	161–192

Table 2 Loadings from a principal component analysis based on five behavioural descriptors of Cape fur seal foraging trips in Namibia in 2002 and 2004.

Variable	PC1	PC2
T_{Trip}	-0.59	0.19
T_{Max}	-0.54	-0.38
$T_{MaxDepth}$	-0.47	0.15
$D_{Start-end}$	0.19	0.75
T_{Land}	-0.33	0.49

Table 3 Mean foraging trip duration (T_{Trip}, h), maximum foraging time (T_{Max}, h) and distance between trip start and end ($D_{Start\text{-}end}$, km) of Cape fur seals (2002 and 2004) partitioned by four geographic zones of the northern Benguela Current Ecosystem (see Figure 1), and per tagging colony. Standard errors are given in parentheses.

	Zone				Colony		
	1	2	3	4	Cape Frio	Cape Cross	Atlas Bay
T_{Trip}	7.5 (2.2)	4.8 (1.3)	4.3 (1.5)	7.9 (2.1)	6.6 (0.4)	4.9 (0.2)	5.8 (0.4)
T_{Max}	51 (3)	28 (1)	27 (1)	35 (5)	31 (3)	48 (1)	96 (2)
$D_{Start\text{-}end}$	38.4 (14.7)	59.7 (9.3)	52.9 (7.0)	144.7 (22.0)	31.3 (12.7)	48.5 (6.1)	95.7 (11.0)

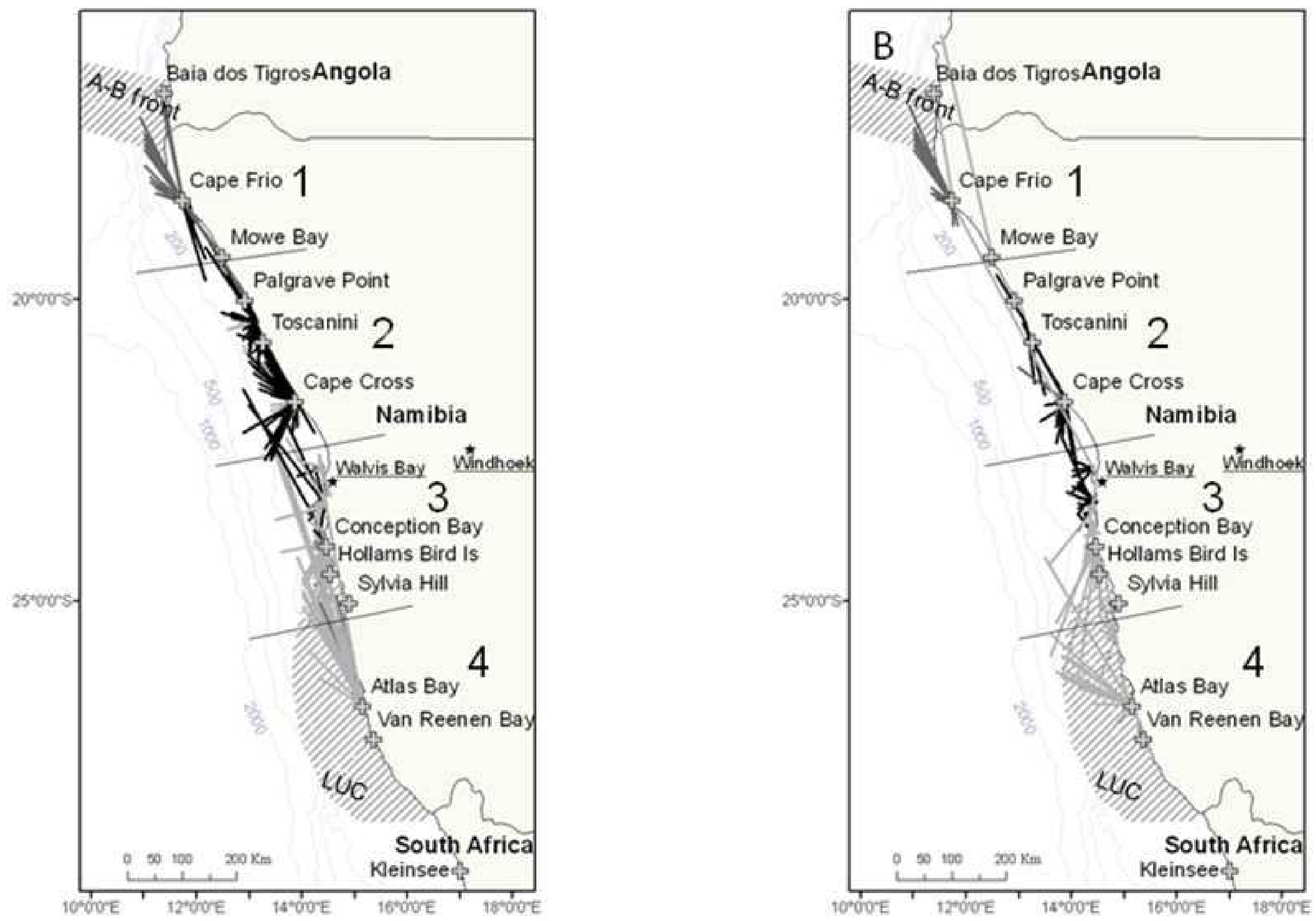

Figure 1 Foraging trips of Cape fur seal females (A) and males (B) tagged at the Cape Frio (dark grey), Cape Cross (black) and Atlas Bay (light grey) colonies in Namibia in 2002 and 2004. Trips are depicted as straight lines between the start location and the location where the seals spent most time during a trip (i.e. T_{Max}). The lines bisecting the coastline partition the northern Benguela Current Ecosystem into geographic zones 1–4; hatched areas in the north and south indicate the Angola-Benguela front and the Lüderitz upwelling cell, respectively.

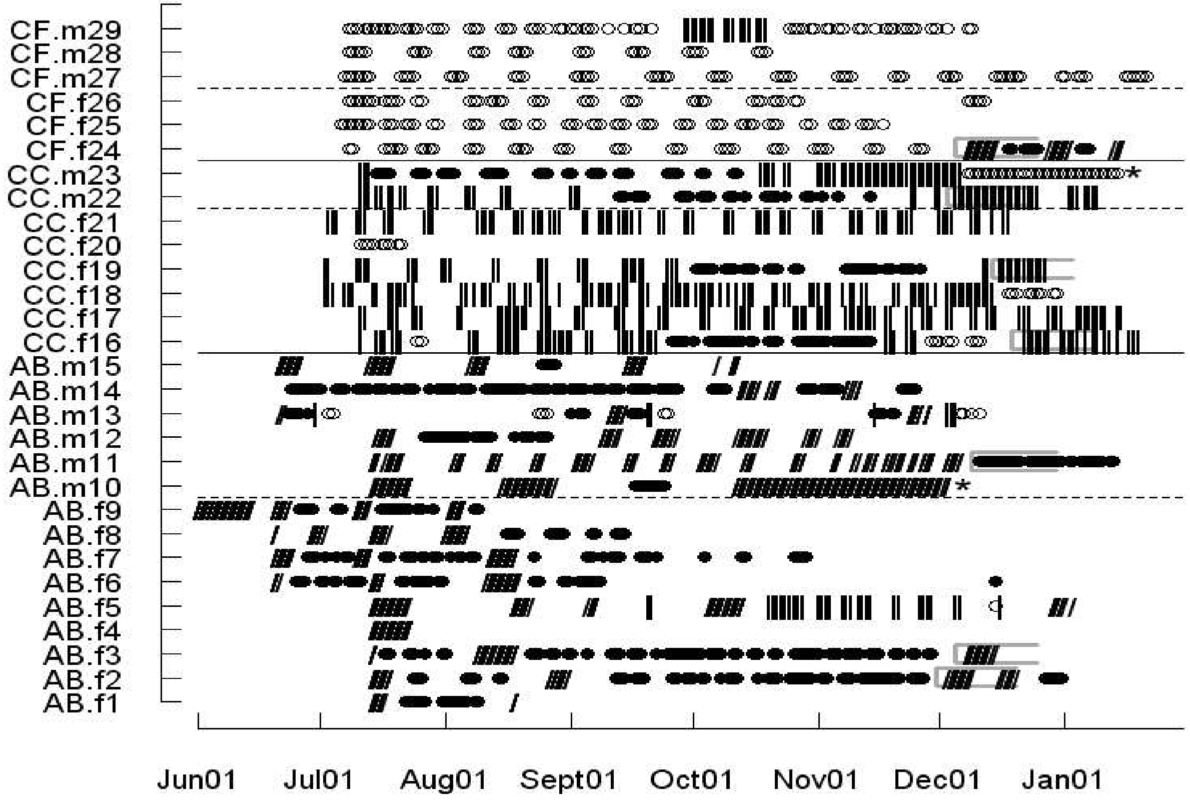

Figure 2 Land attendance patterns by Cape fur seals tagged at Cape Frio (CF), Cape Cross (CC) and Atlas Bay (AB) colonies in Namibia in 2002 and 2004. The scatter plot summarises locations received when the study animals were on land, and symbols indicate land attendance in zone 1(o), zone 2 (|), zone 3 (•) and zone 4 (/), respectively. Labels on Y-axis denote individual study animals (1–29), tagging colony and sex (f = females, m = males). Grey lines indicate extended land attendance possibly indicating breeding; * denotes suspected loss of transmitter.

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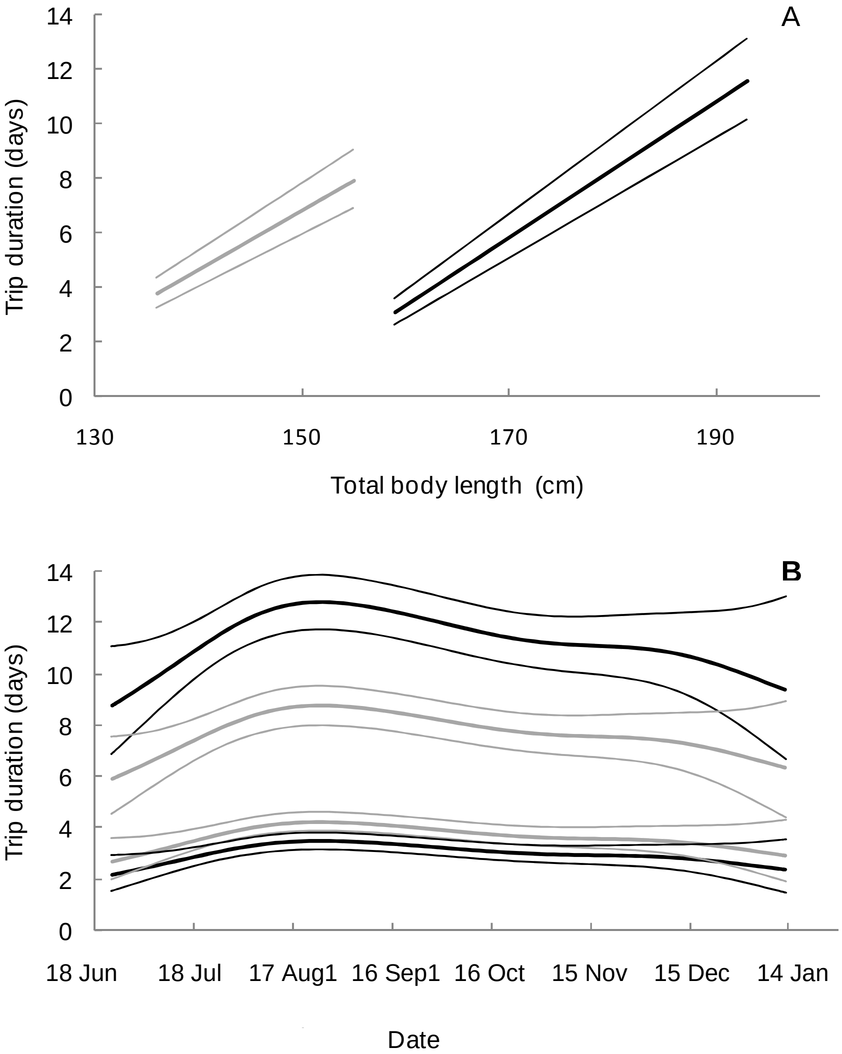

Figure 3 Predicted foraging trip duration of female (grey lines ± SE) and male (black lines, ± SE) Cape fur seal study animals in Namibia in 2002 and 2004, according to the selected GAMMs, as a function of (A) total body length, and (B) total body length and date. In (B), predicted values are plotted for the smallest (lower trendlines) and largest (upper trendlines) female and male, respectively.

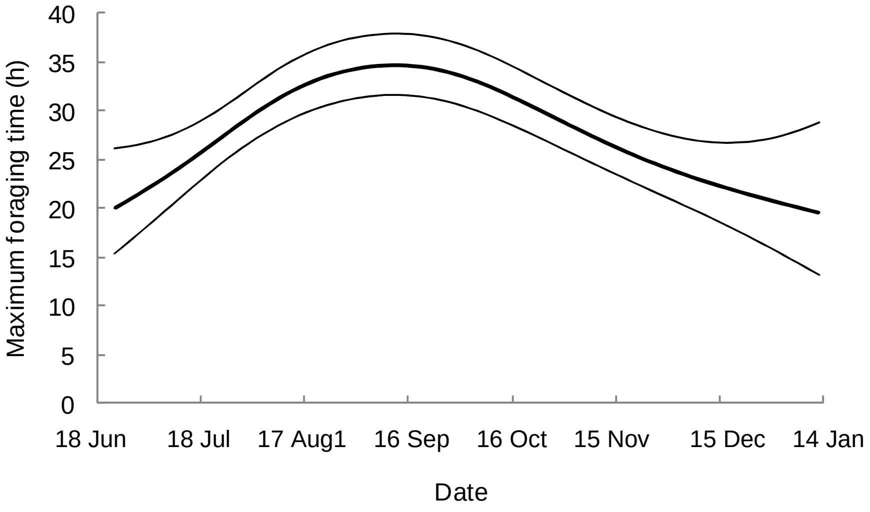

Figure 4 Predicted maximum foraging time (T_{Max}, ± SE) of Cape fur seals in Namibia (in 2002 and 2004) as a function of season, according to the selected GAMM.

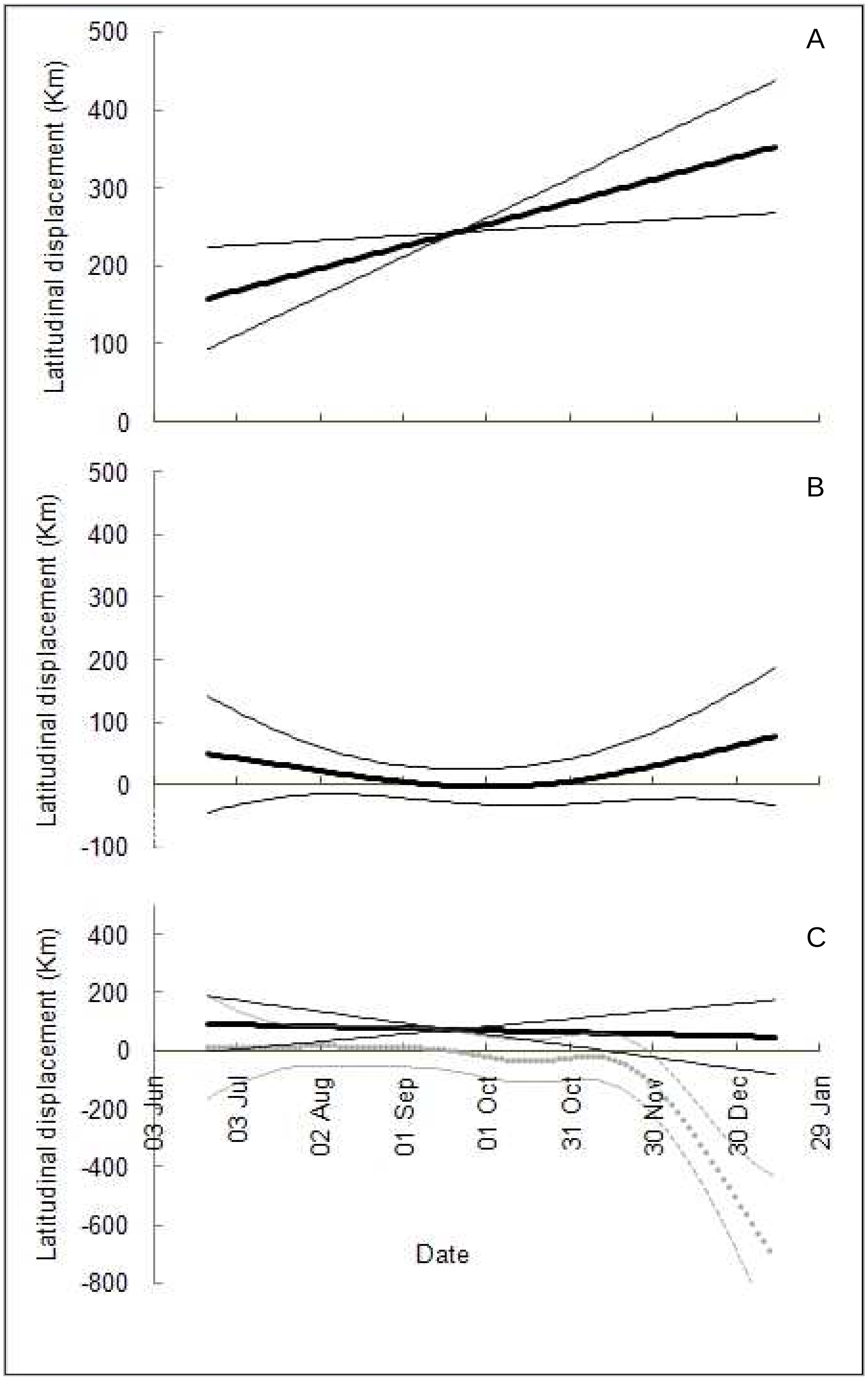

Figure 5 Predicted cumulative latitudinal displacement (L_{Dif}) throughout the study (2002 and 2004) period by seals tagged in (A) Atlas Bay, (B) Cape Cross and (C) Cape Frio in Namibia, according to the selected GAMM. For Cape Frio seals, L_{Dif} is shown with inclusion (dashed light grey line) and exclusion (regular line) of a single female that moved from Cape Frio to Atlas Bay.

CHAPTER 6

Distributional shifts of the dynamic Cape fur seal breeding population in southern Africa, based on aerial censuses (1971–2009)

Abstract

A time series of aerial censuses of Cape fur seals colonies spanning four decades and the three range states, South Africa, Namibia and Angola, was analysed to investigate spatio-temporal changes in population numbers and to attempt to understand the causes and potential management implications of changes. A quantile regression approach was used to estimate trends in pup numbers that were used as proxies for numbers of breeding animals at colonies. There was a 74 % increase in the number of breeding colonies over the study period, with the number in 2009 being 40. There was a significant northward shift in the geographical distribution of the breeding population which was attributable to the dynamic situation in the northern Benguela Current Ecosystem. There, seal numbers declined at most colonies in the south of Namibia, while several new breeding colonies developed and grew in northern Namibia and southern Angola. Effects of environmental variability mediated through prey availability appear to be the most important cause of distributional shifts but other factors, especially human interference, may also have played important roles. Fewer new breeding colonies were established in the southern Benguela Current Ecosystem, corresponding with South Africa, which may be partly attributable to the relatively developed state of the coastline. Despite range expansion and the development and growth of new colonies, the overall size of the population appeared to have been stable since the 1990s. To improve understanding of the drivers of seal population dynamics (including distinguishing between human- and climate-related effects on trends in population size and distribution) requires region-wide monitoring of population parameters to complement aerial census data. Developing and implementing such a programme will be challenging considering divergence in management policies regarding seals between the three range states. Other areas relevant to research, monitoring and possible management intervention are potential effects of new seal colonies on human livelihoods (e.g. fishing) and the conservation of other top predators (threatened seabird species).

Keywords: Angola, *Arctocephalus pusillus pusillus*, Benguela, distribution, Namibia, population, shift, South Africa

Introduction

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, mostly in the Benguela Current Ecosystem (Chapter 2). It was thought that historically, breeding colonies occurred almost exclusively at island locations, with terrestrial predators including humans generally preventing viable breeding colonies from occurring on the mainland (Rand 1972). However, the uncontrolled seal harvesting (sealing) that took place between the 17th and 19th centuries led to the extirpation of seal breeding colonies at several islands (Rand 1952, 1972, Shaughnessy 1984, David and van Sittert 2008). For decades afterwards, many of these islands were managed for the production of seabird products (especially guano) to the exclusion of seals, therefore re-colonisation could not occur (Rand 1963a, 1963b). Around the middle of the 20th century breeding colonies were established at mainland locations, such as at Kleinsee in South Africa and at 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, were accountable 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 programme in the early 1970s to monitor the distribution and abundance of Cape fur seals by way of aerial photographic censuses, there have been changes in the population's environment and in its management: Sealing ceased in South Africa in 1990. Although sealing has been ongoing in Namibia until the end of this study in 2009, it was discontinued at several island locations in the 1970s and 1980s (Wickens *et al.* 1991) and is currently practiced at only at three mainland colonies (Kirkman and Lavigne 2010). Human occupation of several "guano islands" ceased, opening them up to potential re-colonisation by seals (Shaughnessy 1984). In addition, there were substantial changes in the distribution and abundance of the prey species of seals in the Benguela Current Ecosystem (van der Lingen *et al.* 2006). It has been speculated how such developments might impact the distribution of the seal breeding population (Shaughnessy 1984, Chapter 2). Indeed, since the 1990s, changes in the distribution of the population have been observed, with substantial numbers of pups being born at several locations where seals were previously extinct, or where breeding activity was previously negligible or absent (Chapter 3).

Considering the number of well-documented management issues concerning seals (David and Wickens 2003, Makhado *et al.* 2006, Mecenero *et al.* 2007), changes in the distribution of the population are of interest to scientists, managers and interested stakeholders (conservation groups, and others). However, whatever their direct consequences for management may be, distributional shifts in the seal population may be symptomatic of a range of different or inter-related processes. Understanding these is not only relevant to the management of seal-related issues, but is also broadly applicable to the understanding of ecosystem dynamics and therefore to the benefit of ecosystem-based management.

The foremost goal of this study was (1) to report on changes in the spatial distribution of the seal breeding population, especially since the initiation of aerial photographic censuses in the 1970s. To assess these distributional shifts properly required (2) that abundance was also taken into account, so I investigated numerical trends at breeding colonies, using pup numbers as a proxy. In assessing numerical patterns in space and time, I attempted (3) to gain some insight into processes underlying the distributional shifts in the breeding population and the establishment of additional colonies. Furthermore, I aimed (4) to discuss the implications of the observed geographical shifts in the seal population for its research and management.

Methods

Aerial censuses

From the early 1970s until 2008, aerial censuses of Cape fur seal colonies were conducted at intervals of one to five years throughout the breeding range of the population, by researchers of South Africa's Department of Environmental Affairs (DEA).

These censuses rely on the fact that seal pupping is highly synchronised, with most pups being born in a three-week period from late-November to mid-December (Shaughnessy and Best 1975). The censuses were conducted towards the end of the seal breeding season (between 16 and 24 December). Aerial photographs were taken of the breeding colonies. On these, the numbers of new born pups were counted to assess the size of the colonies (Chapter 2). Details on the equipment and techniques used for aerial photography and counting of Cape fur seals are given in Annex 1 of this thesis.

The pups were focused upon in counting because they are the only age class that is constrained to land, whereas an unknown proportion of non-pups are at sea at any one time, therefore counts of the latter are not necessarily representative of true numbers (Shaughnessy 1987). The pup counts underestimate the true numbers of pups born: mortality occurs between birth and the time of the census, some pups are not visible in the photographs, and some births occur after the census (Wickens *et al.* 1991). These and other potential weaknesses of the method are discussed in Annex 1 (Section 2.6). Nevertheless, pup counts are considered to provide the best available index of changes in pup production between years (Shaughnessy 1987) and of the total population size of seals (Wickens and Shelton 1992). During most censuses, the coastline was scanned for the formation of new seal colonies in remote areas. Also, to monitor the formation of new breeding colonies, existing "non-breeding" colonies were checked for the presence of pups and the numbers of non-pups at these colonies were counted in many years.

In this study, censuses were referred to by the year in which they were conducted (so the census conducted in December 2003 was the 2003 census). In 1971, the first year in which a comprehensive census[9] of seal breeding colonies was conducted, the census was conducted during 4–6 December, earlier than the remainder of the time series; in previous analyses, a correction factor was applied to this census, based on observed changes in pup numbers at Seal Island (False Bay) during one summer (Shaughnessy and Best 1975, Shaughnessy 1987). Because the adjusted values for some colonies seem anomalous, I disregarded the 1971 census in this study and considered census results from 1972 onwards. In 2005, the mode of photography used during censuses was converted from black and white monochrome film to digital colour photography. To ensure consistency in the time series of counts, all counts conducted on digital images were divided 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 (DEA unpubl. data).

Breeding and non-breeding colonies

At the time when aerial censuses of seal colonies commenced in the early 1970s, 23 breeding colonies were reported (Shaughnessy 1987). These are listed in Table 1 as "existing" breeding colonies. A Cape fur seal breeding colony was defined by Oosthuizen and David (1988) as any location where more than c. 100 pups were counted on a regular basis. They defined a non-breeding colony as any location where an aggregation of seals regularly occurred but where no

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[9] A census during which at least two thirds of known breeding colonies were covered successfully (Chapter 2).

pups were observed, or where pup counts were less than c. 100. The definition was based on assumptions regarding the number of births required before a colony assumes the social structure of a functional breeding colony, and for a colony to be sustainable in the face of mortality rates and in the absence of immigration. As no evidence was provided to support either assumption the definition was arbitrary, but its use was continued in this study, partly for lack of a more suitable alternative and for convenient comparison with past studies. I used the predictions of a weighted quantile regression model 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 terms of numbers of births, by attaching less weight to anomalously low counts in the time series. The weighted quantile regression model is explained in the following sub-section.

Rates of numerical change at colonies

I assessed trends in pup production for the 23 breeding colonies that existed at the start of the aerial census time series, and at other colonies where breeding was initiated subsequently. For convenience, these two sets of colonies were referred to throughout as “existing” and “additional” colonies, respectively. Note that some of the “additional” breeding colonies formed at locations of extinct seal colonies, and that some of the “existing” colonies occur at sites where seal breeding colonies were absent historically.

Assessing trends in pup counts at Cape fur seal colonies was problematical because the variable pattern in pup counts between years, especially since the early 1990s (e.g. Chapter 2). 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: large-scale mortality of new born pups prior to the aerial census (de Villiers and Roux 1992, Kirkman *et al*. 2006); 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 size of the population of breeding-age females and create artificially small values that obfuscate the true trend in abundance. In a conventional trend analysis, these small values drag the trend line below the true level. What is required to address this problem is an analysis tool which objectively constructs a trend line through the larger values which are believed to represent the true population sizes. I achieved this 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 (LR) (Cade and Noon 2003).

Specifically, I computed the regression of the 95th quantile so that less emphasis was placed on anomalously small counts in the time series that reduced the explanatory powers of growth trends and generated smaller predictions. 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

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

where j is year 1, 2,….i, commencing from the first census year for each colony, t is the target year and 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, decreasing exponentially in both directions so that the fifth year on either side of the target year has weight 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. The weighted regression was therefore effectively based on counts made in the target year and the five years on either side of it. A smaller weighting function giving consequence for example only as far as four years on either side of the target year would have resulted in unreliable predictions where gaps of five years or longer 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 "additional" colonies, gaps of up to 10 years without data occurred. For these colonies it was necessary to set the smoothing constant at 7.0 to prevent nonsensical predictions. These colonies were Geyser Rock, Marshall Reef (both "existing" colonies) and Torra Bay, Pelican Point, Dolphin Head, Buchu Twins, Cape Columbine, Sylvia Hill and Klein Ichaboe (all "additional" colonies).

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 the former constructs a trend line that represents the upper 95th percentile, so passes among the larger values in the time series, whereas the latter generates a trend line passes through the middle of the values in the time series. Effectively the RQ model places greater emphasis on the large values, the LR model places equal emphasis on all values. For comparison with the outcomes of the RQ models, I also applied LR models to the pup data, using the same weighting functions. For the reasons given above, the RQ-predicted pup values were expected to be the better indicators of numerical trends for the population (all age classes) than those predicted by the LR models.

The analyses were done by the statistical software package R version 2.9.0 (R Development Core Team), incorporating the “quantreg” package (Koenker 2009). Results were reported per colony for the entire time series that was considered, but to aid with distinguishing general patterns in space and time, they were also summarised for two subsets of the time series (up to, or after, 1990, effectively splitting the time series under consideration into two periods) and for various subsets of colonies. Colonies were grouped by country, according to the type of colony (island or mainland), their status at the start of the time series (i.e. “existing” or “additional”) or into five geographical zones that were indicated in Figure 1. Table 1 indicates which of these groups were applicable to each colony.

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, the number of breeding colonies in existence (determined by weighted regression models on the pup count time series of the colonies), and the “along the path” distance around the coastline of each these colonies from a fixed point. Woody Cape (33°46.03’S, 26°19.45’E), the eastern boundary of Algoa Bay, was used as the fixed point (Figure 1), because all known Cape fur seal colonies are westward of this point. The “centre of distribution” (CoD) of the breeding population in each year was estimated as

$$\mathrm{CoD} = \frac{\sum(\quad n)}{\sum} \qquad (2)$$

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). This was to avoid auto-correlation 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. an “additional colony such as Cape Frio was considered only from when the predicted pup count exceeded 100). The above analyses were repeated for several subsets of the population, namely the populations to the north (“northern sub-population”) and south (“southern sub-population”) of the Orange River, island and mainland colonies, and colonies occurring in the five geographical zones indicated in Figure 1 and Table 1.

Results

Temporal changes in pup numbers

Of the 45 colonies presented in Table 1, 40 are currently breeding colonies based on the application of the RQ model to the times series of pup counts per colony and considering the definition of Oosthuizen and David (1988). According to this approach therefore, 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 aerial censuses, four, including Marshall Reef, Robberg, Jutten Island and Möwe Bay did not fulfil the definition of a breeding colony at the time of the most recent comprehensive census (2008). Another colony, Mercury Island, remained extinct after seals were displaced from there in the late 1980s.

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 (Figure 2, “existing” South African colonies; Figure 3, “existing” Namibian colonies; Figure 4, “additional” South African colonies; Figure 5, “additional” Namibian and Angolan colonies), although RQ models were less sensitive to variability in pup numbers and the annual numerical predictions of the RQ models were generally larger than the LR model predictions (Appendix 1).

Average rates of change in numbers at each colony for the first and second halves of the time series, are provided in Table 1, and Table 2 provides a breakdown of the estimated rates of change for the various groupings of colonies over the two halves of the time series and over the entire time series, in terms of the proportions of colonies in these groups that experienced a positive average rate of change in each period. Because 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 three periods (Pearson's r: 1972–2008 = 0.99, 1972–1990 = 0.88, 1991–2008 = 1.00), only the results of the RQ models were presented or summarised in these two tables. In the early period all the groups of colonies except for zone 1 were characterised by positive growth among all or most of their constituent colonies (Table 2). However, in the later period, the percentage of colonies with positive growth was considerably reduced for nearly all the groups that were considered. Only about one quarter of "existing" colonies were associated with net positive growth in the later period, on average, compared with nearly 80 % of the "additional" colonies. Correspondingly, the only two zones where "additional" colonies numbered more than "existing" colonies in the later period (zones 3 and 5) were the only zones associated with positive growth for most of their constituent colonies (Table 2).

The smaller of South Africa's nine "existing" colonies were generally associated with fluctuations about zero in the rates of change of colony size over the time series, whereas the four largest South African colonies (Kleinsee, Seal Island in False Bay, Geyser Rock and Elephant Rock) were associated with growth in the first part of the time series, that declined to zero or below zero in the later period (Figure 2, Appendix 1A). Most of the "existing" Namibian colonies were associated with positive growth in the first half of the time series, then negative growth during the 1990s, and in the late 1990s and 2000s, either fluctuations of the rates of change about zero or continuing negative growth (Figure 3, Appendix 1B). At some of these colonies, including Marshall Reef, van Reenen, Bay and Lion's Head, growth that occurred during the first period appeared to be entirely reversed during the second period.

"Additional" breeding colonies in South Africa and Namibia with time series of 15 years or longer (including non-census years in between), such as Cape Frio, Sandwich Harbour, Klein Ichaboe, Paternoster Rocks, Bird Island and Buchu Twins, generally grew rapidly initially, with growth rates exceeding 40 % per annum during the first period (Table 1), but their growth rates declined and stabilised around zero towards the end of the time series (Figures 4 and 5). Growth trends were difficult to establish at some of the other "additional" colonies, on account of one or some combination of the following: a lack of data points (e.g. North Reef, Toscanini), substantial fluctuations in pup counts with zero values in some years (e.g. Dolphin Head, Conception Bay), or the fact that censusing only commenced after breeding was already firmly entrenched at some colonies (e.g. Cliff Point, Baia dos Tigros). However, most of these colonies were associated with positive growth. One of the recently established "additional" colonies, Vondeling Island, had a growth rate of c. 120 % per annum (Table 1).

When summing the predicted values of all colonies each year, the results of both model types indicate that there has been little or no growth since the early 1990s, with regard to the entire region and the northern sub-population, with negative growth occurring during the early 1990s (Figure 6). The results indicate that positive growth in the southern sub-population continued to increase until the early 2000s, before numbers declined. This largely reflected the trend at the largest colony, Kleinsee (Appendix 1A) which accounted for c. two thirds of pup numbers in South Africa in 2000, dropping to c. 50 % in 2006 and further to c. 44 % by 2008, according to both models. Two more of the four largest "existing" colonies in South Africa showed similar declines, namely Seal Island in False Bay and Elephant Rock (Appendix 1A). With regard to the northern sub-population, there was a considerable shift in the ratio of numbers between zones 4 and 5 – both model types showed a c. 17 % decrease in the ratio of pup numbers between zones 4 and 5, from 1990 to 2008.

Changes in spatial distribution based on pup numbers

As in Tables 1 and 2, only the results based on predictions of RQ regression models are displayed in Figure 7, showing the shifts in the CoD and range of the seal breeding population at six year intervals from 1976 to 2006. Whereas the eastward range of the breeding population remained constant throughout the time series, the northward range was extended by c. 680 km (from Cape Cross to Baia dos Tigros in southern Angola) during the latter part of the time series (Figure 7.1). There was a significant shift in the CoD of the breeding population over the entire range, at a rate of 5.82 km/year (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 northern population (Figure 7.2) was implicit in the northward extension of the entire population, but the range of the southern population was also extended northward during the time series (Figure 7.3), by c. 105 km (from Kleinsee to Buchu Twins). However, whereas the shift in CoD of the former subset was significant (7.20 km/year, SE = 1.39, $F_{1,4}$ = 26.66, p = 0.006, R^2 = 0.87), the latter was not (0.30 km/year, SE = 0.67; $F_{1,4}$ = 0.23, p = 0.66, R^2 = 0.05).

The northern range of the population breeding on islands was extended considerably (c. 1 050 km) by the establishment of a breeding colony at the island in Baia dos Tigros, but overall there was no significant change in the CoD of this subset of the population (-3.35 km/year, SE = 1.69; $F_{1,4}$ = 3.94, p = 0.12, R^2 = 0.50), because the northward range extension was counterbalanced by the establishment of "additional" island colonies in the south of the range (Figure 7.4). The northern range of the population breeding on the mainland was extended by c. 465 km (from Cape Cross to Cape Frio) and the CoD of this subset of the population shifted significantly northward (7.95 km/year, SE = 1.84; $F_{1,4}$ = 19.03, p = 0.012, R^2 = 0.83) (Figure 7.5). Of the five geographical zones (Figure 7), a significant (northward) directional shift in the CoD occurred only in zone 5 (4.35 km/year, SE = 1.29; $F_{1,4}$ = 11.43, p = 0.028, R^2 = 0.74), where "additional" colonies established both to the north and south of the only "existing" colony in the zone (Cape Cross).

Discussion

As was the case with fur seal populations elsewhere that have recovered from past over-exploitation (e.g. Boyd 1993, Arnould *et al.* 2003, Hofmeyr *et al.* 2006) there is interest with regard to the dynamics of the Cape fur seal population including trends in distribution and abundance, the relationship to the distribution and abundance of the pristine (or pre-sealing) population, and the population size in relation to the carrying capacity of the environment (e.g. Butterworth *et al.* 1988, Chapter 3). Chapter 2 concluded from trends in pup production that the population growth that occurred up to 1993 (reported by Butterworth *et al.* 1995) stabilised subsequently, and that the population in 2003 was similar in size to 10 years previously. However, mainly "existing" colonies were considered. Increases in pup production in the 1990s and 2000s at several locations previously classified by Oosthuizen and David (1988) as non-breeding colonies (e.g. Buchu Twins, Pelican Point and Conception Bay), and the establishment of other "additional" breeding colonies such as Baia dos Tigros and Cliff Point, were not taken into account. This was because several of these locations had not been censused frequently or at all up until 2003. This assessment includes all colonies at which births have been recorded during aerial photographic censuses conducted since 1971, and includes five extra years of data compared to Chapter 2.

Several studies have inferred population size and trends (all age classes) from pup numbers (e.g. Hofmeyr *et al.* 2005, Kirkwood *et al.* 2005, Hofmeyr *et al.* 2006). The main aims of this study were to report on the establishment of several new breeding colonies and assess spatial shifts in the breeding population though time, for which it was necessary to determine numerical trends at individual colonies. However, by summing the values predicted by the regression models for all individual breeding colonies in each year of this study, it was possible to look at trends in predicted pup numbers for the entire region and for subsets of the population (Figure 6). Although the predicted values and the consequent trends differ between the two model types (RQ and LR), both support that there has been little growth in the population, relative to the early 1990s, in spite of the shifts in distribution and the development of several new breeding colonies.

Present versus historical distribution of the seal population

Generally, knowledge of the pre-sealing state of seal populations is dependent on the availability and accuracy of anecdotes and records by historical sealers and explorers (Best and Shaughnessy 1979, Arnould 2002). Based on such information (discussed in Rand 1972, Best and Shaughnessy 1979, Shaughnessy 1984), it seems that the distribution of the Cape fur seal population in the pre-sealing era closely mirrored the distribution of islands in south and western southern Africa. These are distributed between Algoa Bay, South Africa, and Hollam's Bird Island, Namibia (Figure 1) (Baia dos Tigros in southern Angola became an island in about 1973, before this it was joined to the mainland by a sand spit, Simmons *et al.* 2006). Rand (1972) thought that the most northern colony in the pre-sealing range was at Cape Cross, but this was disputed by Best and Shaughnessy (1979) who thought it unlikely that this mainland colony could have been established before the 19th century, and that therefore the northernmost colony in the pre-sealing era was c. 355 km farther south at Hollam's Bird Island.

By the late 19th or early 20th century, at least 26 Cape fur seal colonies had become extinct as a result of uncontrolled sealing initiated in the 17th century (Rand 1972, Best and Shaughnessy 1979, Shaughnessy 1980a, 1982, 1984, David and van Sittert 2008). About 90 % of these colonies occurred on islands, which varied widely in size, between c. 1 ha to 500 ha (median = c. 6.5 ha). During the sealing era, refuge for the population was provided at several small (< 3 ha), relatively inaccessible islands which were unprofitable for sealers (Rand 1952, Stewardson 1999). Most of the island colonies that existed in 1971 (n = 17, see Table 1) probably constituted such "remnant" colonies, although three of them (Seal Island in False Bay, Sinclair

Island and Albatross Rocks) were among the 23 colonies that were driven to extinction, and were re-established in the late 19th or early 20th century (Shaughnessy 1984).

If all of the island colonies in existence at the start of this study period, and all of the known colonies that were extinct at this time, were breeding colonies in the pre-sealing era, the number of breeding colonies then would have been similar to the present (c. 40). However, this estimate for the pre-sealing era may be inflated: it was uncertain whether all the extinct colonies were breeding colonies, or whether all the island breeding colonies existing at the start of this study were breeding colonies in the pre-sealing era. Some of these islands (e.g. Black Rocks, Seal Island in Mossel Bay and Robbesteen) are small, low-lying and exposed to rough sea conditions, frequently becoming inundated or virtually inundated in heavy swells (Rand 1972, Stewardson 1999). Drowning of pups by rough seas may account for large inter-annual fluctuations in pup counts at such locations (Appendix 1A). Given the poor survival prospects for pups at such locations and the availability of space at larger islands (Chapter 3), many small island locations may not have been utilised for breeding historically, until seal colonies were displaced from more favourable locations by sealing.

Irrespective of what the exact number of colonies in the past was, the distribution of the present population is different to the pre-sealing era. Besides the loss of most of the larger islands off the coast as breeding habitat, it is certain that the overall distribution of the present population is substantially farther northward than in the past, considering the recent development of mainland breeding colonies in northern Namibia and southern Angola, and also considering that approximately three quarters of the known locations of extinct seal colonies occur in South Africa. Furthermore, there was little evidence for mainland colonies occurring in the pre-sealing era: only four (including one at Cape Cross and three in South Africa) have been mentioned in historical records (discussed in Shaughnessy 1982, Shaughnessy 1984, Stewardson 1999), which is one quarter of the number of mainland breeding colonies in the current population (this study). It was uncertain whether these four colonies were breeding or non-breeding colonies in the pre-sealing era.

Possible causes of spatio-temporal changes during the study period

Roux (1987) classified the process of re-colonisation of the Amsterdam Islands by the subantarctic fur seal *A. tropicalis*, following depletive human exploitation, into four phases: (1) A "survival" phase extending from the cessation of exploitation to the initiation of breeding, whereby 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 “re-colonisation” phase during which numbers increased and new colonies arose in response to a shortage of space in the founding colonies; (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 over-exploitation, including subantarctic fur seals at Marion Island (Hofmeyr *et al*. 2006), New Zealand fur seals *A. forsteri* on the Otago Peninsula (Bradshaw *et al*. 2000) and South American sea lions *Otaria flavescens* in Patagonia (Grandi *et al*. 2008). These descriptions involved populations situated on oceanic islands or on mainland peninsulas, which were localised relative to the extensive range of the Cape fur seal population. Broadly, the model seems applicable to the expansion of the Cape fur seal population since the early 20th century (when sealing was placed under legal controls, Shaughnessy 1984), but as discussed below, the “re-colonisation” phase appears to have been considerably influenced by factors that were not density dependent.

The persistence of “remnant” Cape fur seal 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 Sinclair Island (by the late 19th century) and of Albatross Rocks and Seal Island in False Bay (before the 1950s) possibly marked the beginning of the “re-colonisation” phase. At the time, seals were being prevented from re-occupying 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). However, new seal breeding colonies developed on the mainland, including at Wolf Bay, Atlas Bay and Kleinsee, 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).

With the exception of the breeding colonies at Cliff Point and North Reef, which were discovered by researchers after they were mature breeding colonies, all sites where “additional” breeding colonies occur were known to have been utilised by non-breeding seals initially (Shaughnessy 1987, Oosthuizen and David 1988, DEA unpublished data), including immature and senescent animals. Non-breeding seals also hauled out in numbers at Atlas Bay and Wolf Bay, before breeding colonies were established at these locations (Rand 1972). Development of non-breeding colonies and their transition to breeding colonies have been shown to be a characteristic of the "re-colonisation" phase in other otariid populations, and have been attributed to saturation of space at source breeding colonies (e.g. Bradshaw *et al.* 2000, Grandi *et al.* 2008). With regard to the Cape fur seal population, Oosthuizen and David (1988) proposed that there may be other causes for the development of non-breeding colonies than exclusion of animals from crowded breeding colonies. These included convenience of haulout sites with respect to feeding grounds, and disturbance at breeding colonies (e.g. due to sealing). Such effects may operate synergistically, not only with regard to the formation of non-breeding colonies, but also with their transition into breeding colonies and their further growth. The possible mechanisms for the establishment and growth of "additional" breeding colonies are discussed below.

Breeding space limitation (density dependent paradigm)

At mainland Cape fur seal colonies, breeding space does not appear to be a limiting factor (Wickens *et al.* 1991, pers. obs.); however, all island colonies that were in existence in the 1970s are on small islands (3 ha in area or less) and typically are extremely crowded, especially during the breeding season (Rand 1967, Crawford and Best 1990, pers. obs.). Therefore, limited breeding space was a probable mechanism of density dependence at these island locations, most of which have shown little or no sustained growth during this study (Figures 2 and 3).

Cape fur seal females generally show fidelity to their natal and breeding sites (Rand 1967), behaviour that is typical among pinniped species (e.g. Gentry 1998, Pomeroy *et al.* 2000, Raum-Suryan *et al.* 2002). As expounded by Matthiopoulos *et al.* (2005), such fidelity can slow down colonisation of new habitat by seals and prevent populations from utilising all available habitats in their range, despite conditions of resource limitation. The northern fur seal *Callorhinus ursinus* population, for example, colonised only two new locations in 200 years (Gentry 1998). With regard to the Cape fur seal population, a case in point was the situation in Algoa Bay, where the only current seal colony is limited to Black Rocks, a group of four exposed rocks, the largest of which has a surface area of less than 1 ha and is used for breeding (Rand 1972). This colony was thought to have survived sealing operations of previous centuries only on account of its inaccessibility (Stewardson 1999). Nearby in the same island group are two larger islands, Seal Island (c. 6.5 ha) and Stag Island (c. 1.1 ha), where seal colonies existed until they were completely destroyed in the 19th or early 20th century (Shaughnessy 1984, Stewardson 1999). Yet despite that there has been no growth at Black Rocks during the study period (Appendix 1A), seals have as yet not re-colonised the other two islands, which are not inhabited by humans. Circumstantially, such evidence as well as the northward gradient in the distribution of new seal colonies (Figure 7), suggest that factors other than breeding space limitation may be accountable for the observed proliferation of breeding colonies over the study period.

Prey availability (mechanistic paradigm)

While density-dependent factors are known to influence seal population dynamics, several authors have emphasised the importance of environmental variability as a density independent influence on the population dynamics of seals (e.g. Trillmich 1993, Gerber and Hilborn 2001, Matthee *et al.* 2005, Forcada *et al.* 2005, Reid and Forcada 2005). In a productive yet highly variable marine system such as the Benguela Current Ecosystem (Shannon *et al.* 1988), which largely corresponds with the range of the seal population, limits of prey resources may be influenced by extrinsic factors such as spatio-temporal effects of environmental variability, and also fishing. Effects of such stressors can reduce the carrying capacity of local environments, and because adult female fur seals (on which the burden of parental care wholly rests) are central place foragers that must locate prey within a limited geographic range of their breeding colony to reproduce successfully (Lea *et al.* 2006), the effects can conceivably cause dispersal in search of new home ranges, where dispersal is defined as a one-way movement in an unpredictable direction in search of resources (Shields 1984).

South Africa’s marine environment (including prey resources) was considered to have been generally stable during the study period and its commercial fish stocks appeared to have benefited from conservative fisheries management strategies that were implemented in this time (Cury and Shannon 2004, van der Lingen *et al.* 2006). Nevertheless, wide-scale shifts in the distributions of certain species targeted by commercial fisheries have occurred during the study period. Notably, the overall resource availability of adult sardines *Sardinops sagax* and West Coast rock lobster *Jasus lalandii* shifted from the west coast to the south coast, east of Cape Town (i.e. from zone 3 to zone 2, see Figure 1) (Fairweather *et al.* 2006, Cockcroft *et al.* 2008) and there was an abrupt eastward shift in the stock of Cape anchovy *Engraulis encrasicolus* adults in 1996, that persisted to the end of the study period (Roy *et al.* 2007). The distributions of several seabird top predator species in South Africa that prey on these groups (e.g. Cape gannet *Morus capensis*, Cape cormorant *Phalacrocorax capensis*, bank cormorant *P. neglectus*, swift tern *Sterna bergii*), as well as several other seabird species that do not (e.g. crowned cormorant *P. coronatus*, Hartlaub's gull *Larus hartlaubii*), have also shifted eastward during the study period (Crawford et al. 2008a, 2008b). Considering the congruency in their timing and direction, Crawford et al. (2008b) proposed that these shifts may have been influenced by environmental factors, possibly forced by climate changes.

Because the prey species that have undergone geographical shifts are also preyed upon by seals, it has been proposed that the progressive distributional shifts of these prey away from the west coast may have resulted in nutritional stress to the seal population in South Africa (Makhado *et al.* 2006), the bulk of which occurs on the west coast. Cape fur seals are generalist predators that feed on a large variety of prey species (David 1987, Mecenero *et al*. 2006), unlike seabird species including the Cape gannet, Cape cormorant, swift tern and African penguin *Spheniscus demersus*, which feed mainly on anchovy and sardine in the southern Benguela Current Ecosystem (Underhill and Crawford 2007). Therefore the seal population may be relatively buffered against reduced availability of these prey species (compared with seabird species).

However, numerical declines at the Kleinsee and Elephant Rock seal colonies in the north of zone 3 since 2000 (Figure 2, Appendix 1A) and the simultaneous development and rapid growth of the colony at Vondeling Island farther south (Figure 4, Appendix 1C), suggest that shifts in prey availability may well have affected the distribution of the seal breeding colony in South Africa, at least between 2000 and 2009. The only "additional" breeding colony south of Vondeling Island is the small colony at Duikerklip at the western edge of zone 2, although a non-breeding colony was also established in zone 1 at Robberg (Plettenberg Bay, see Figure 1) in the 1990s, and may develop into a breeding colony in future. The lack of "additional" breeding colonies on the south coast (zones 1 and 2) may be an artefact of a lack of suitable breeding habitat for seals in this area; the current seal breeding colonies on the south coast are on a few small island locations (< 3 ha) that appear to be at carrying capacity (Figures 2 and 4, Appendix 1A and 1C) and there is no other suitable island habitat in this area that is not human-occupied except for islands at the far east of the range, in Algoa Bay.

Furthermore, there is probably less scope for breeding colonies to establish on the mainland of the south coast compared with the largely restricted or reserved coastlines of Namibia and the north of South Africa's west coast (Shaughnessy 1982), where the potential for human interference is lower (Shaughnessy 1982). All the current mainland breeding colonies, including most of the "additional" breeding colonies, occur in the latter areas, giving rise to the northward (clockwise in relation to the coast) shift in the population (Figure 7). With reference to Figure 7 which has the Orange River as a proxy for the boundary between the southern and northern parts of the Benguela Current Ecosystem (van der Lingen *et al.* 2006), it was clear that the northward shift in the distribution of the population during the study period was mainly attributable to the development of "additional" breeding colonies in the northern Benguela Current Ecosystem (i.e. in Namibia and southern Angola). In zone 5, which includes southern Angola and northern Namibia, c. 90 % of the current breeding colonies are "additional" colonies (see Table 1) and at least three of these (Cape Frio, Torra Bay and Pelican Point) increased at rates greater than 20 % per annum during the latter half of the study (Table 1). These rates of increase can only have been sustained by continued immigration of breeding animals from other breeding colonies, because the maximum intrinsic annual rate of increase of seal populations is c. 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).

The obvious source of immigrants to zone 5 colonies is from zone 4 colonies, where numbers declined more or less proportionally to the increase in zone 5. Zone 4 contains nearly all of the "existing" Namibian colonies (with the exception of Cape Cross in zone 5), most of which were characterised by variable recruitment during the second half of the time series (1991–2009, Appendix 1B) with associated negative rates of change during this period or at least during the 1990s (Table 2, Figure 3). Environmental perturbations in the northern Benguela Current Ecosystem between 1993 and 1995 (Gammelsrød *et al.* 1998), exacerbated by over-fishing (Boyer and Hampton 2001), were responsible for depletion of fish stocks (including prey of seals such as sardine, anchovy, Cape horse mackerel *Trachurus trachurus capensis* and hake *Merluccius* spp.). Reduced pregnancy rates and survival rates (especially of pups) were attributed to the resulting unfavourable feeding conditions (Anselmo *et al.* 1995, Roux 1998) and led to low pup counts (Appendix 1B). Prey resources for top predators remained in a depleted state until the end of the study period, especially in southern and central Namibia (Cury and Shannon 2004, van der Lingen *et al.* 2006). The Lüderitz upwelling cell which coincides approximately with zone 4 (Figure 1) and is the most powerful driver of ocean productivity in the northern Benguela Current Ecosystem (Bakun 1996), was characterised by below average upwelling volumes from the early 1990s to the end of the study period (Peard 2007). The poor upwelling was likely to have been the ultimate driver of the cascade of unfavourable environmental conditions observed in Namibia (Peard 2007). A further consequence of the unfavourable environmental conditions was that the distributions of certain prey stocks shifted northward (Boyer and Hampton 2001, van der Lingen *et al.* 2006) and, in particular, the availability of horse mackerel for fisheries and top predators in the north of Namibia increased (Axelsen *et al.* 2004, Mecenero *et al.* 2007).

In Chapter 5 it was shown that study seals from Atlas Bay displayed foraging behaviour indicative of poor feeding conditions (long foraging trips, low fidelity to their tagging colony and to foraging areas, displacement to other colonies) during 2002–2004. Almost invariably, their foraging routes were to the north of Atlas Bay and the colonies to which they re-located were most commonly Conception Bay and Sandwich Harbour, though some seals moved farther north to Pelican Point, Cape Cross, Torra Bay, Cape Frio and Baia dos Tigros. In contrast, seals tagged at Cape Frio in the north generally displayed fidelity both to their colony and to foraging areas, suggesting reliable prey resources nearby. This contrasting pattern between results in the north and the south was consistent with the known distribution of prey in the northern Benguela Current Ecosystem following the depletion of prey stocks in the south caused by environmental changes and fishing. Therefore the interpretation of the study was that seal behaviour reflected a general gradient of improving feeding conditions from south to north in the northern Benguela Current Ecosystem.

The available evidence therefore supports the hypothesis that the effect of environmental variability, mediated through prey availability, was likely to have played an important role in the spatio-temporal changes in the seal numbers in the northern Benguela Current Ecosystem observed in this study, in particular the contrasting trends in seal abundance between colonies in zones 4 and 5 and the development and rapid growth of “additional” breeding colonies in the latter. Such effects have also been documented for pinniped populations elsewhere. For example, seal and sea lion populations of the eastern Pacific Ocean rim were severely affected by prey depletion associated with an el Niño event in the 1980s (Trillmich and Ono 1991). This resulted in large-scale mortality, population declines, dispersal from unproductive areas and the establishment of several new colonies.

<u>Human disturbance</u>

Human disturbance was identified by Rand (1972) as a causal factor in the development of new seal breeding colonies, even after sealing became regulated at the beginning of the 20th century. Examples were the establishment of the colonies at Atlas Bay and Wolf Bay prior to the study period (Rand 1972), the establishment of a colony on Mercury Island in the mid-1980s (Crawford *et al.* 1989), the subsequent displacement of this colony to the mainland (Chapter 3), and a large influx of seals to Cape Cross in late 1980s (Wickens *et al.* 1991). Except for the establishment of a breeding colony at Dolphin Head in Namibia, which occurred at the same time as seals were being driven off nearby Mercury Island in the interests of conserving seabird colonies (Crawford *et al.* 1994, Chapter 3), the links made between human disturbance and breeding dispersal was largely anecdotal. However, in each case (except for the establishment of Dolphin Head), it was known that human disturbance at the purported source colonies was in the form of sealing that took place during the breeding season (i.e. November–December), the time of year when seal colonies are most vulnerable to disturbance (Boren *et al.* 2002). In Chapter 4, it was shown that relatively benign disturbance (compared with sealing-related disturbance) caused by researchers in localised study sites at Atlas Bay caused breeding animals to disperse from these sites. Therefore it is probable that sealing-related disturbance during the breeding season (at the colony scale) would have induced breeding dispersion to other locations, consistent with the theory that intense, repetitive human disturbance of animals that associate humans with predation risk should result in a shifting of habitat (Frid and Dill 2002).

After a moratorium was placed on sealing in South Africa in 1990 (Wickens *et al.* 1991), the likelihood of human disturbance sufficiently intense to induce dispersal of breeding animals, diminished. In Namibia, where sealing was ongoing at the end of the study period, the sealing season was closed at the start of the breeding season each year since 1990, to avoid disruption of breeding (Morton *et al*. 2007). Nevertheless, sealing occurred on most days over a period of four to four and half months leading up to the breeding season at the three colonies that were targeted since 1990 (Cape Cross, Wolf Bay and Atlas Bay), and it can be assumed that stress was induced in the animals that survived each operation (including lactating females) by the disturbance associated with sealing (Kirkman and Lavigne 2010).

Gentry (1998) demonstrated experimentally (using the northern fur seal *Callorhinus ursinus*) that despite inherent site fidelity, breeding fur seal females are flexible enough to re-locate under sub-optimal conditions such as when stress is induced by human disturbance, as long as there is a group of conspecific animals to disperse to. In Namibia, the latter stimulus was available at colonies previously considered to be non-breeding colonies by Oosthuizen and David (1988), such as Pelican Point, Sandwich Harbour, Conception Bay and Cape Frio, all of which occur on the mainland and are not space-limited. It is therefore a reasonable hypothesis that sealing disturbance has played a role in the development and growth of breeding colonies at these locations and other locations such as Torra Bay and Sylvia Hill, during the study period.

Sythesis

Whereas the estimated overall trend in pup numbers towards the end of the study period (Figure 6) was suggestive of a population having attained an equilibrium state, the "maturity" phase of Roux's (1987) model, the evidence from the numerical patterns of individual colonies pointed to a dynamic situation characterised by highly variable rates of change both within and between colonies, with apparently negative growth at several colonies in the south of Namibia (zone 4) and the north of South Africa (in zone 3), and the development of several "additional" colonies, especially in northern Namibia and southern Angola (zone 5) and the west coast of South Africa (zone 3). Distinguishing between possible causal factors for the observed patterns was not straightforward and was confounded by continued direct or indirect human interference during the population's "re-colonisation" phase, including sealing and related disturbance (Best 1990, Wickens *et al.* 1991, Kirkman and Lavigne 2010). It was also hindered by a lack of long term information on performance attributes (e.g. offspring survival, attendance patterns) that was representative of the population's range and could have supplemented information from pup counts (Kirkman 2007).

The lack of growth or a stabilization of the rates of change at several of the small "existing" breeding colonies, especially in South Africa (e.g. Black Rocks, Seal Island in Mossel Bay Jacob's Reef, Quoin Rock) was consistent with a limitation of breeding space at such colonies. However, inter-annual fluctuations in counts at many such locations may be attributable to extrinsic factors such as variable intensity of storms during the breeding season prior to the timing of the aerial census (Stewardson 1999, Kirkman *et al.* 2006), a density independent effect. In general, density dependence has rarely been positively identified at the scale of populations, including pinniped populations (McLaren and Smith 1985, Reid and Forcada 2005), a difficulty that has been attributed to confounding effects of environmental processes on density processes (Krebs 2002). This is relevant to a dynamic marine system such as the Benguela Current Ecosystem, and seems to be reflected in the current dynamic state of the seal population, especially in the northern Benguela Current Ecosystem. Here, the congruent negative trends and pronounced fluctuations in the rates of change at many of the “existing” breeding colonies in zone 4 (Figure 3, Appendix 1B), including colonies that were subjected to sealing during the last 20 years (Wolf Bay and Atlas Bay) and those that were not, indicated common causality such as effects of environmental variability on prey availability. However, it is feasible that environmental variability, density and human interference have all played a role, perhaps a complementary role, in the spatio-temporal dynamics of the seal population observed during the study period.

Considerations for research, monitoring and management

To those with a management interest in the Cape fur seal population, determining population size and predicting future population size is of particular value (e.g. Butterworth and Wickens 1990, Butterworth *et al.* 1995). The ability to project future population size depends upon a density dependent relationship to determine equilibrium population level. However, Reid and Forcada (2005) pointed out that reaching this equilibrium will not occur if the primary forces driving population dynamics are not density dependent, and therefore that studying relationships between population dynamics and mechanistic driving forces may be of most relevance. This entails a holistic approach that is inclusive of determinants at larger spatial scales than the scale of density-dependent effects, for example at an ecosystem scale.

In this regard, recommendations for a seal research and monitoring programme of relevance to ecosystem-based management of marine resources (inclusive of the seal population itself) throughout the Benguela Current Ecosystem are provided in Chapter 8. These include region-wide monitoring of key demographic parameters (including continuation of aerial censuses) and of performance and behavioural attributes of seals that can be related to environmental or other biological variables. Such monitoring is essential for improving our understanding of the drivers of the seal population dynamics (including distinguishing between human- and climate-related effects on trends in population size and distribution), and investigating effects of seal population dynamics on human livelihoods and the conservation of other top predators in the region.

The implementation of such a programme will be challenging given the differences between the three nation states with regard to policy on seal population management. In 2010, these are summarised as follows. Angola, into where the range of the seal breeding population extended during the latter part of this study, made a decision to cull seals from 2010, to alleviate the perceived competitive effects of seals with regard to fisheries (M. Morais pers. comm.). In Namibia, seals are hunted annually for commercial profit according to a quota system (Roux and Sakko 1997). In South Africa, seals are utilised as a non-consumptive resource (ecotourism) (DEAT 2007) and are not culled for the sake of fisheries (Cochrane *et al.* 2004). To facilitate co-operation between researchers of the three countries, the Benguela Current Commission (BCC), a multi-sectoral initiative between the governments of the countries that has within its objectives the promotion of integrated management and protection of the environment using an ecosystem approach to ocean governance, has recommended that the implementation phase of the proposed monitoring programme be supported by their Science Programme (BCC 2009).

Management concerns regarding shifts in the distribution of the seal population include potential implications for fisheries and for other top predators. Whereas the former has long been a prominent topic of research and debate in the Benguela Current Ecosystem (e.g. Butterworth *et al*. 1988, Wickens *et al*. 1992), the latter is a relatively recent issue with regard to interactions between seals and locally breeding seabirds that have poor conservation status (Kemper *et al.* 2007, BirdLife International 2010), including the Cape gannet (vulnerable), the African Penguin (endangered) and the bank cormorant (endangered) (Chapter 3, du Toit *et al.* 2003). Seal-seabird interactions that are detrimental to seabird populations include predation by seals in the vicinity of seabird colonies (du Toit *et al.* 2004, Makhado *et al.* 2006) and competition for breeding space between seals and seabirds (Frost *et al.* 1976, Shaughnessy 1980b, Crawford *et al.* 1989). Although seal and seabird colonies co-existed on many of the islands off southern Africa before large-scale sealing commenced in the 17th century, the latter have apparently been placed at a competitive disadvantage by the subsequent modifications to the islands, such as the removal of refuges and nesting material by guano scraping (Shaughnessy 1984). Thus, re-colonisation by seals of guano islands with important seabird colonies is potentially a serious conservation concern.

During the study period, at least two guano islands were re-colonised by seals, namely Mercury Island (1980s) and Vondeling Island (2000s). The growth rates of seal numbers at these two colonies over periods of a few years (average annual rates of over 100 %, see Figures 3 and 4, Table 1) illustrated that even though seals have been slow to re-colonise guano islands, their growth rates when they do return can be extremely rapid. In South Africa, the government's Policy on the Management of Seals, Seabirds and Shorebirds (DEAT 2007) provides for safeguarding of seabird breeding habitat at islands by removing seals through programmes of deliberate displacement or by construction and placement of artificial barriers. However, displacing seals off Vondeling Island, where important African penguin and bank cormorant colonies exist (Crawford *et al.* 1999, Underhill *et al.* 2006), was, by 2008, no longer a viable management option. Firstly, with nearly 9 000 pups counted there in 2008, the breeding colony at Vondeling Island was already 40 % larger than the breeding colony at Mercury Island was in 1987 (Appendix 1D), before seals were finally removed from there (Crawford *et al.* 1994). Secondly, such an intervention at Vondeling Island risked displacing large numbers of seals to other island locations of sensitive seabird breeding habitat (five occur within a c. 30 km radius of Vondeling Island), in the same way as displacement of seals from Mercury Island led to the establishment of a new breeding colony Dolphin Head in Namibia.

Two management options were available at Vondeling Island: prevent further expansion by seals into certain seabird breeding areas at the island using barriers and/or disturbance; alternatively allow continued growth of the seal colony at this island to take its course and concentrate conservation efforts on preventing seal re-colonisation of other guano islands. Provided such interventions occurred early in the process, while the seal population is composed of non-breeding individuals that haul out at the water’s edge, re-colonisation can be discouraged without inflicting injury or mortality, or incurring great cost (Crawford *et al.* 1989). In zones 2 and 3, Vondeling Island and other islands in nearby Saldanha Bay (Figure 1) are the only known island locations of historical seal breeding colonies that are currently unoccupied by humans and therefore constitute obvious sites for expansion of the seal breeding population. If separation of seal colonies from seabird breeding habitat is to be continued as a seabird conservation management tool, as stated in the policy (DEAT 2007), prevention of seal re-colonisation in its early stages or before it can commence should be seen as a priority, especially considering the recent histories of Mercury and Vondeling Islands and the potential financial, logistical and animal welfare implications of trying to keep seal and seabird colonies apart at locations where they co-exist. For this, the manning of certain islands may be necessary.

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Table 1 The location 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 1971, in clockwise order with regard to the coastline, starting at the southeastern-most colony. Colonies marked with superscript E were “existing” breeding colonies in 1971; I or M under “Type” refers to “island” or “mainland” colonies respectively; “zone” refers to geographical regions to which colonies were assigned (see Figure 1). 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 rates of change for colonies where more than 100 pups have been counted during at least one census, are shown; of these colonies, the names of those that did not fit the definition of a breeding colony in 2008 based on the prediction of the weighted quantile regression equation, are italicised (n = 5). Colonies 1–18 occur in South Africa, 19–44 in Namibia and number 45 in Angola.

	Name of breeding colony	Latitude (south)	Longitude (east)	Type	Zone	Mean rate of change (± SE) 1972–1990	Mean rate of change (± SE) 1991–2008
1.	Black Rocks ^{E}	33°50.27	26°15.80	I	1	-0.0212 ± 0.0205	0.0100 ± 0.0804
2.	*Robberg*	34°60.00	23°23.13	M	1		
3.	Seal Is. (Mossel Bay) ^{E}	34°09.02	22°07.02	I	1	-0.0087 ± 0.0080	-0.0194 ± 0.0320
4.	Quoin Rock ^{E}	34°47.23	19°40.10	I	2	0.0034 ± 0.0219	-0.0169 ± 0.0324
5.	Geyser Rock ^{E}	34°41.32	19°24.75	I	2	0.0431 ± 0.0060	0.0016 ± 0.0050
6.	Seal Is. (False Bay) ^{E}	34°08.30	18°35.00	I	2	0.0306 ± 0.0090	-0.0148 ± 0.0318
7.	Duikerklip	34°03.50	18°18.13	I	2	0.1405 ± 0.1108	0.1601 ± 0.1907
8.	Robbesteen ^{E}	33°38.63	18°24.10	I	3	0.0192 ± 0.0068	0.0127 ± 0.0763
9.	Vondeling Is.	33°09.07	17°58.82	I	3		1.1983 ± 0.2368
10.	*Jutten Is.*	33°04.80	17°57.17	I	3		
11.	Jacob’s Reef ^{E}	32°57.30	17°51.70	I	3	0.0103 ± 0.0060	-0.0186 ± 0.0737
12.	Cape Columbine	32°49.55	17°50.70	I	3		0.0356 ± 0.0415
13.	Paternoster Rocks	32°44.30	17°52.30	I	3	0.3228 ± 0.0796	0.0613 ± 0.1038
14.	Bird Is.	32°05.28	18°18.13	I	3	0.0659 ± 0.0368	0.1853 ± 0.2571
15.	Elephant Rock ^{E}	31°38.63	18°08.65	I	3	0.0659 ± 0.0090	-0.0155 ± 0.0386
16.	Kleinsee ^{E}	29°34.17	16°59.80	M	3	0.0557 ± 0.0145	-0.0052 ± 0.0263
17.	Cliff Point	29°05.90	16°49.10	M	3		-0.1526 ± 5.4728
18.	Buchu Twins	28°45.57	16°33.78	M	3	0.2338 ± 0.0452	0.1412 ± 0.1674
19.	Lion’s Head ^{E}	27°40.33	15°31.40	M	4	0.0403 ± 0.0266	-0.0716 ± 0.1734
20.	Sinclair Is. ^{E}	27°40.00	15°31.30	I	4	-0.0072 ± 0.0078	-0.0098 ± 0.0322
21.	van Reenen Bay ^{E}	27°24.00	15°21.00	M	4	0.0268 ± 0.0220	-0.0462 ± 0.0470

Table 1 (cont.)

	Name of breeding colony	Latitude (south)	Longitude (east)	Type	Zone	Mean rate of change (± SD) 1972–1990	Mean rate of change (± SD) 1991–2008
22.	Black Rock ^{E}	27°23.40	15°21.00	I	4	0.0581 ± 0.0111	-0.0235 ± 0.0655
23.	Albatross Rock ^{E}	27°07.00	15°14.30	I	4	0.0331 ± 0.0269	0.0300 ± 0.0746
24.	North Reef	27°00.00	15°11.40	I	4		0.1728 ± 2.0599
25.	Atlas Bay ^{E}	26°49.92	15°07.90	M	4	0.0385 ± 0.0324	-0.0301 ± 0.0339
26.	Long Is. ^{E}	26°49.33	15°07.20	I	4	0.0455 ± 0.0146	-0.0251 ± 0.0348
27.	Wolf Bay ^{E}	26°48.67	15°07.20	M	4	0.0566 ± 0.0093	-0.0191 ± 0.0212
28.	Dumfudgeon Rock ^{E}	26°29.67	15°07.20	I	4	0.0367 ± 0.0130	0.0173 ± 0.0738
29.	Boat Bay Rock ^{E}	26°25.33	15°05.50	I	4	0.0385 ± 0.0165	0.0035 ± 0.0945
30.	Staple Rock ^{E}	26°21.33	14°59.00	I	4	0.0089 ± 0.0109	-0.0119 ± 0.0313
31.	*Marshall Reef* ^{E}	26°21.60	14°57.60	I	4	0.0569 ± 0.0023	-0.2612 ± 0.0943
32.	Klein Ichaboe	26°17.40	14°55.80	I	4	0.1933 ± 3.0707	0.0849 ± 0.0788
33.	Dolphin Head	25°44.00	14°49.92	M	4		-0.0085 ± 0.1950
34	*Mercury Island**	25°43.17	14°50.10	I	4	1.2476 ± 1.2086	
35.	Sylvia Hill	25°08.03	14°51.15	M	4		0.1427 ± 1.2342
36.	Hollam's Bird Is. ^{E}	24°38.33	14°31.80	I	4	0.0195 ± 0.0245	-0.0119 ± 0.0654
37.	Conception Bay	23°55.80	14°29.40	M	5	0.7553 ± 2.8311	-0.4554 ± 0.7619
38.	Sandwich Harbor	23°21.00	14°28.80	M	5	0.6865 ± 0.2671	0.1213 ± 0.2122
39.	Pelican Point	22°52.50	14°26.60	M	5	0.6591 ± 2.6645	0.4417 ± 0.0806
40.	Cape Cross ^{E}	21°46.50	13°57.00	M	5	0.0731 ± 0.0095	-0.0244 ± 0.0732
41.	Toscanini	19°23.82	13°22.80	M	5		
42.	Torra Bay	19°27.60	13°15.00	M	5		0.2882 ± 0.0026
43.	*Möwe Bay*	19°22.67	12°42.27	M	5		
44.	Cape Frio	18°26.17	12°00.20	M	5	0.4889 ± 0.0474	0.2281 ± 0.0977
45.	Baia dos Tigros	16°38.40	11°43.20	I	5		0.1337 ± 3.7829

* Up to 1986 only, before seals were forcibly removed from the island.

Table 2 Breakdown of the average rates of change in pup numbers at Cape fur seal breeding colonies in South Africa, Namibia and Angola, estimated using weighted 95 % quantile regression models, for the entire region and for various subsets of the population, over the study period (1972–2009), and the first and second parts of the time series (1972–1990 and 1991–2009, respectively). Note: groups with partitions in the first field are exclusive to each other with regard to constituent colonies but non-exclusivity occurs between the partitions. The information provided in Table 1 indicates to which subset(s) each colony was allocated.

Group of breeding colonies	N of colonies in group			Percentage of N showing net increase		
	1972–2008	1972–1990*	1991–2009	1972–2008	1972–1990	1991–2009
Entire region	42	26	42	67	88	50
South Africa (SA)	16	10	16	69	80	56
Namibia	25	16	25	64	94	44
Angola	1	0	1	100	-	100
“Existing”	23	23	23	57	87	26
“Additional”	19	3	19	79	100	79
SA “existing”	9	9	9	56	78	33
SA “additional”	7	1	7	86	100	86
Namibia “existing”	14	14	14	57	93	21
Namibia “additional”	11	2	11	73	100	73
Mainland	17	7	17	65	100	47
Islands	25	18	25	68	89	52
SA mainland	3	1	3	67	100	33
SA islands	13	9	13	69	78	62
Namibia mainland	13	6	13	62	100	46
Namibia islands	12	10	12	67	90	42
Zone 1	2	2	2	0	0	50
Zone 2	4	3	4	75	100	50
Zone 3	10	5	10	80	100	60
Zone 4	18	14	18	56	93	33
Zone 5	8	2	8	88	100	75

* “Additional” breeding colonies that attained breeding status before 1991 based on application of equation 1 to their time series (n = 3), are included among the colonies considered for this time period.

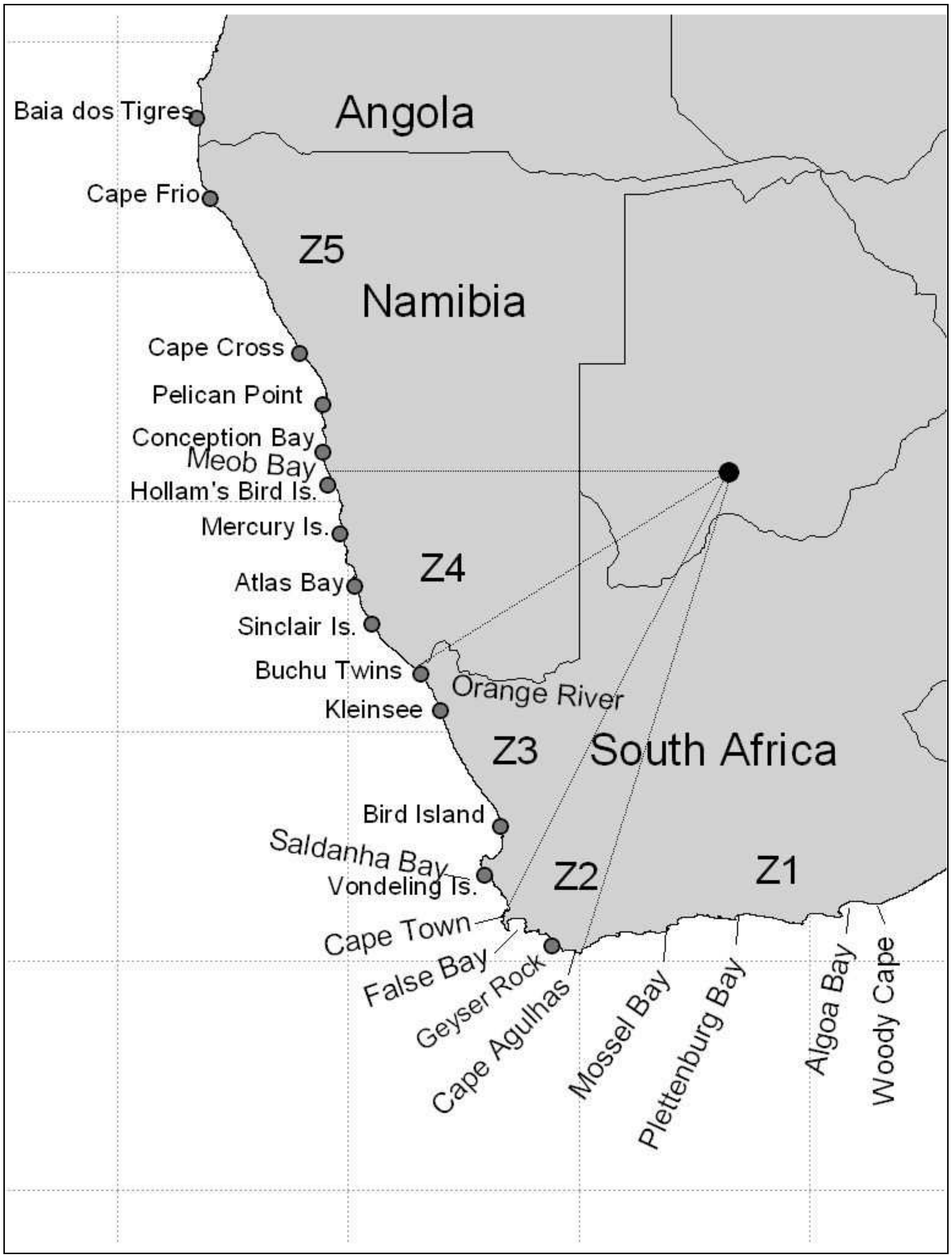


Figure 1 Map showing selected Cape fur seal breeding colonies in South Africa, Namibia and Angola, and macro-scale features mentioned in the text. The lines from the central point to the coastline separate Z1-Z5, which refer to geographical zones into which colonies are grouped in Tables 1 and 2, depending on where they occur on the coastline. Zone 1 is from Cape Agulhas eastward, zone 2 from Cape Agulhas to Cape Town, zone 3 from Cape Town to the Orange River, zone 4 from the Orange River to Meob Bay (approximately coinciding with the position of the Luderitz upwelling cell between 28°S and 25°S, Peard 2007), and zone 5 is north of Meob Bay.

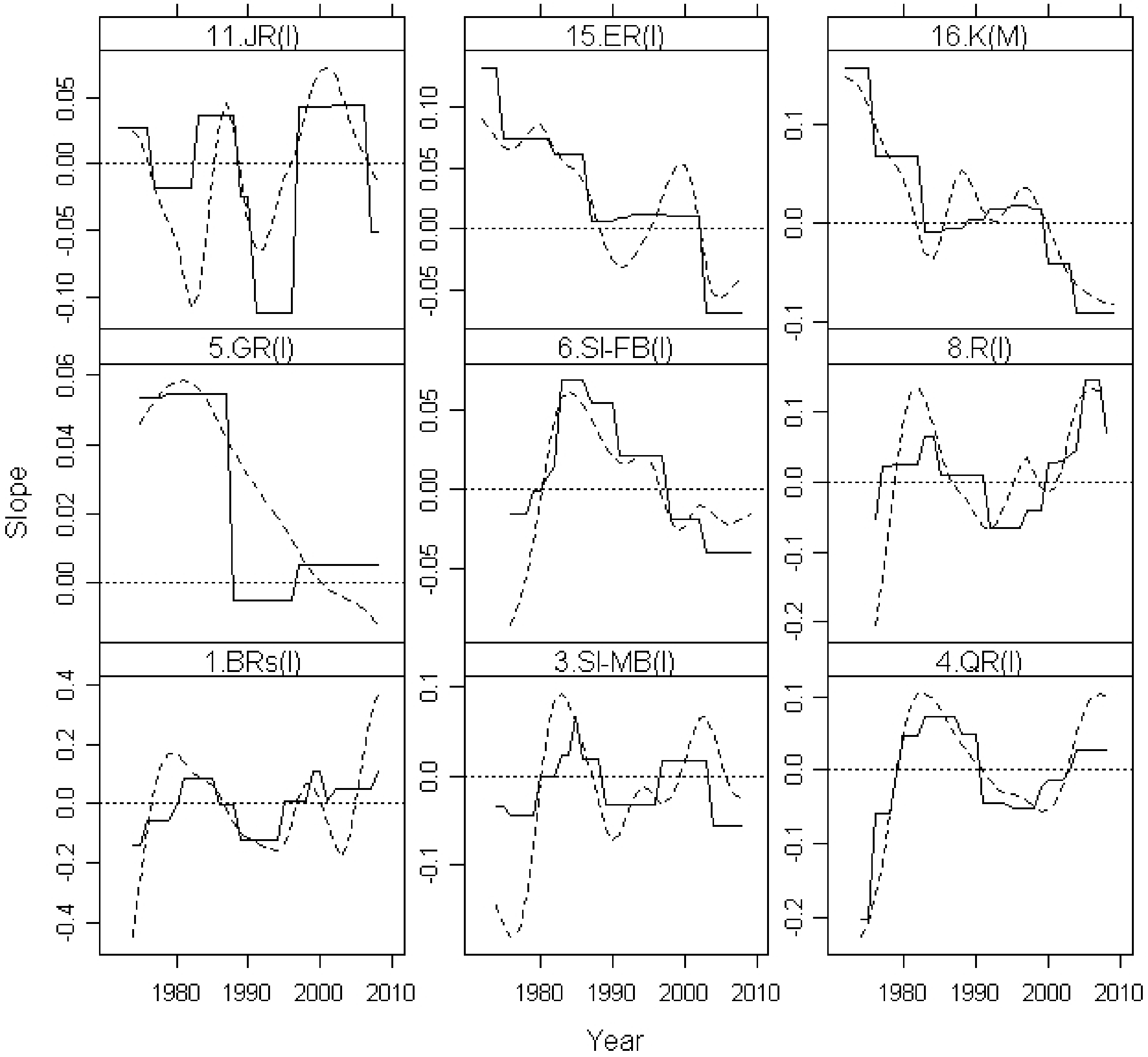


Figure 2 Moving rates of change of pup numbers at Cape fur seal breeding colonies in South Africa that were in existence by 1971 ("existing" colonies), estimated using weighted 95th quantile (solid line) and least squares (dashed line) regression models. The number in the heading of each panel corresponds with the colony numbers in Table 1, and the "I" or "M" in parentheses refers to whether the colony is situated on an island or on the mainland. The abbreviated colony names represent the following: BRS = Black Rocks, SI-MB = Seal Island, Mossel Bay, QR = Quoin Rock, GR = Geyser Rock, SI-FB = Seal Island, False Bay, R = Robbesteen, JR = Jacob's Reef, ER = Elephant Rock, K = Kleinsee.

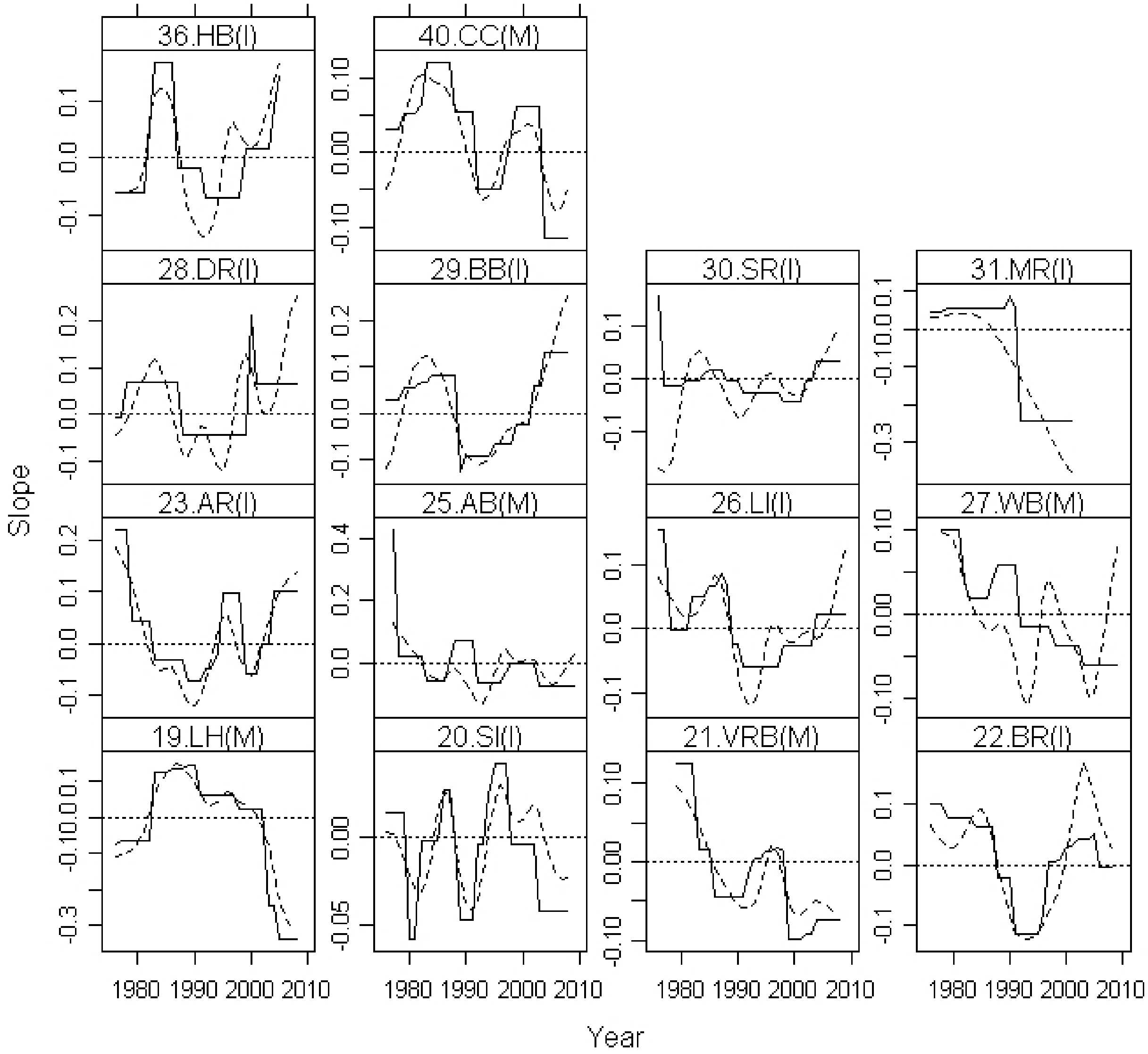


Figure 3 Moving rates of change of pup numbers at Cape fur seal breeding colonies in Namibia that were in existence by 1971 ("existing" colonies), estimated using weighted 95th quantile (solid line) and least squares (dashed line) regression models. The number in the heading of each panel corresponds with the colony numbers in Table 1, and the "I" or "M" in parentheses refers to whether the colony is situated on an island or on the mainland. The abbreviated colony names represent the following: LH = Lion's Head, SI = Sinclair Island, VRB = van Reenen Bay, BR = Black Rock, AR = Albatross Rock, AB = Atlas Bay, LI = Long Islands, WB = Wolf Bay, DR = Dumfudgeon Rock, BB = Boat Bay Rock, SR = Staple Rock, MR = Marshall Reef, HB = Hollam's Bird Island, CC = Cape Cross.

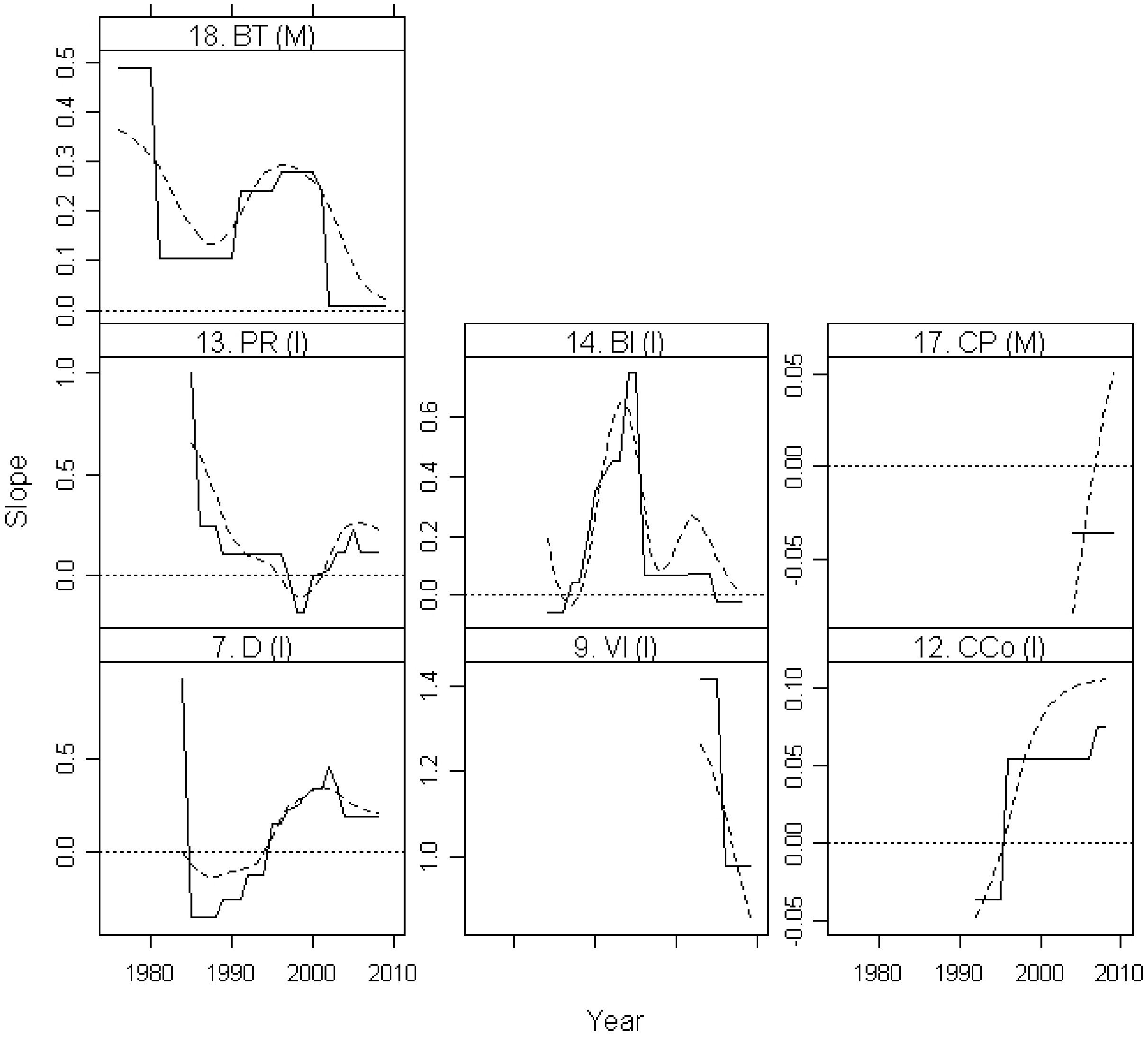


Figure 4 Moving rates of change of pup numbers at Cape fur seal breeding colonies in South Africa that were established after 1971 ("additional" colonies), estimated using weighted 95th quantile (solid line) and least squares (dashed line) regression models. The number in the heading of each panel corresponds with the colony numbers in Table 1, and the "I" or "M" in parentheses refers to whether the colony is situated on an island or on the mainland. The abbreviated colony names represent the following: D = Duikerklip, VI = Vondeling Island, CCo = Cape Columbine, PR = Paternoster Rocks, BI = Bird Island, CP = Cliff Point, BT = Buchu Twins.

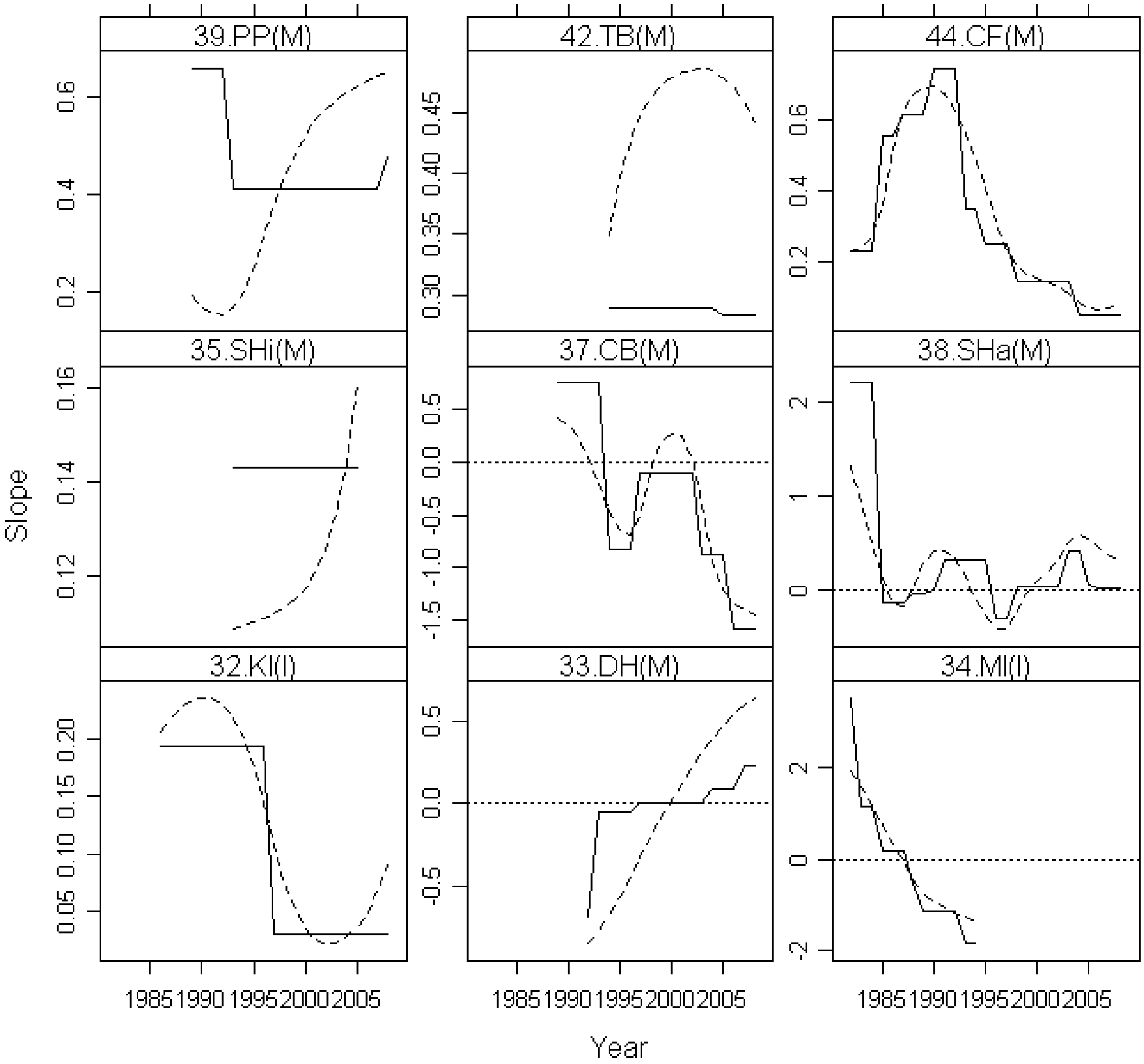


Figure 5 Moving rates of change of pup numbers at Cape fur seal breeding colonies in Namibia that were established after 1971 ("additional" colonies), estimated using weighted 95th quantile (solid line) and least squares (dashed line) regression models. Colonies with two or less data points are omitted (i.e. North Reef, Toscanini and also including Baia dos Tigros in Angola). The number in the heading of each panel corresponds with the colony numbers in Table 1, and the "I" or "M" in parentheses refers to whether the colony is situated on an island or on the mainland. The abbreviated colony names represent the following: KI = Klein Ichaboe, DH = Dolphin Head, MI = Mercury Island, SHi = Sylvia Hill, CB = Conception Bay, SHa = Sandwich Harbour, PP = Pelican Point, TB = Torra Bay, CF = Cape Frio.

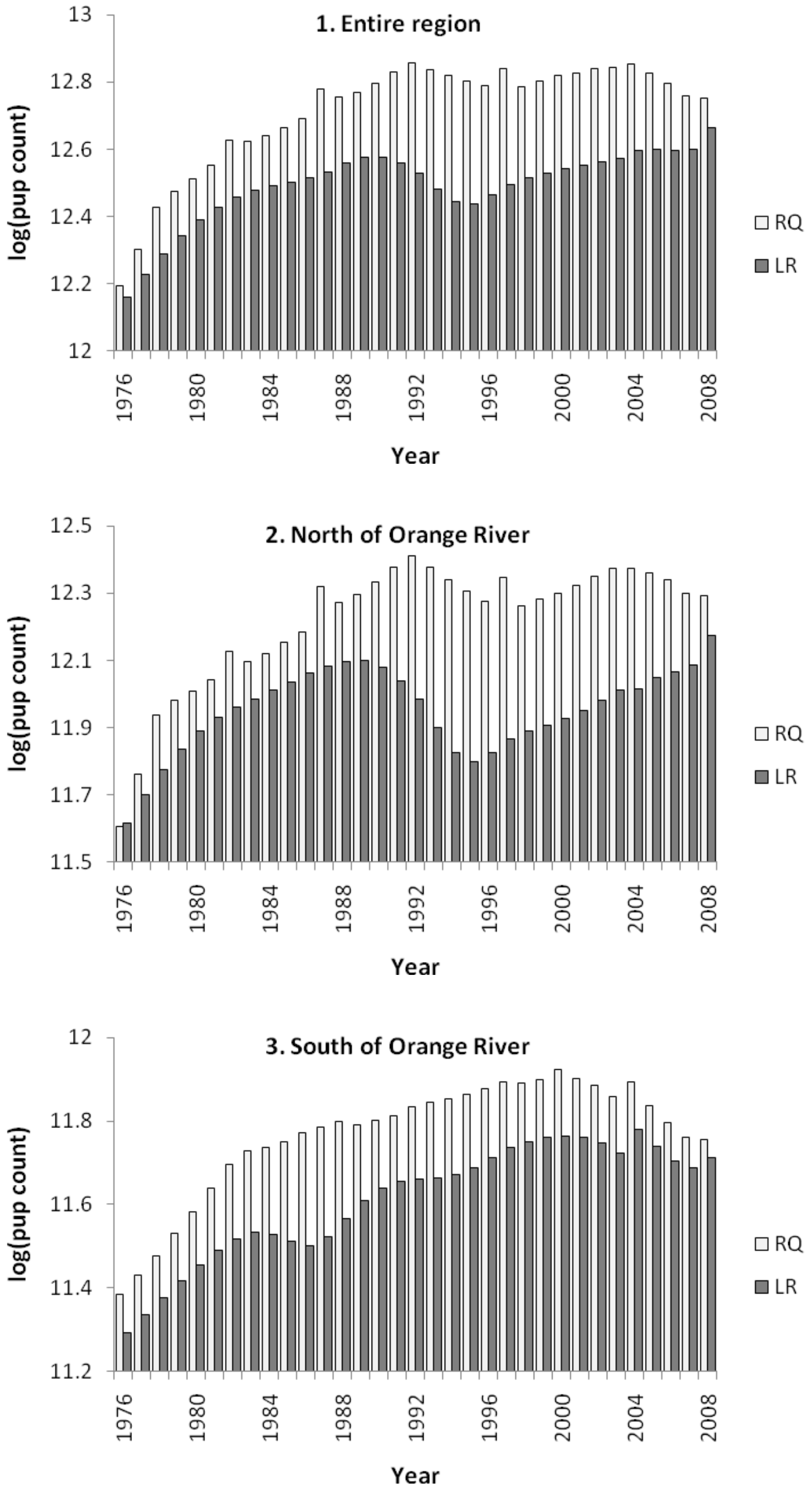


Figure 6 The sums of the predicted number of pups each year for the Cape fur seal breeding colonies in the entire region (1) and for all colonies to the north (2) and south (3) of the Orange River (northern and southern sub-populations, respectively) for 1976–2008, determined using weighted 95th quantile (RQ) and least squares (LR) regression models.

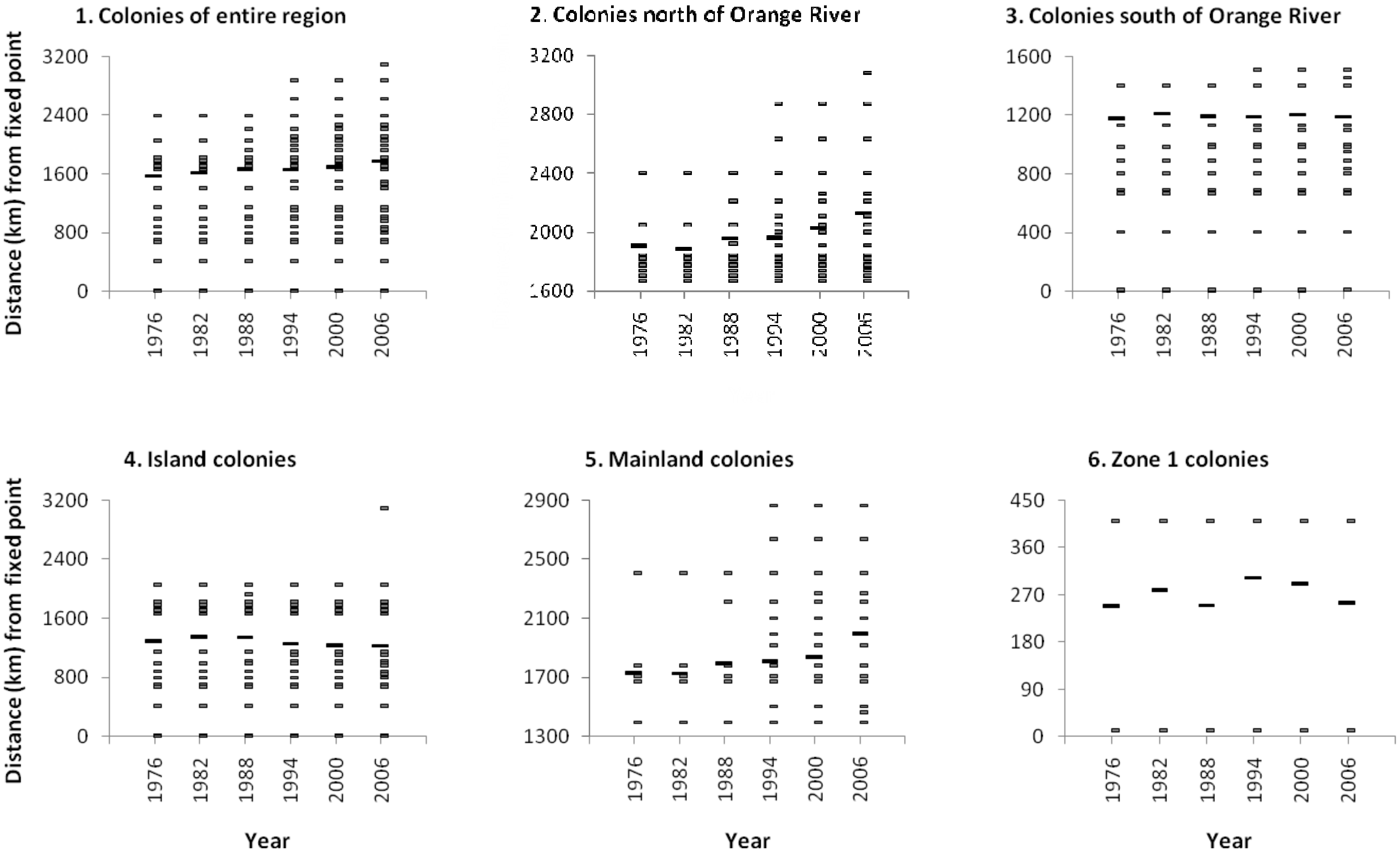
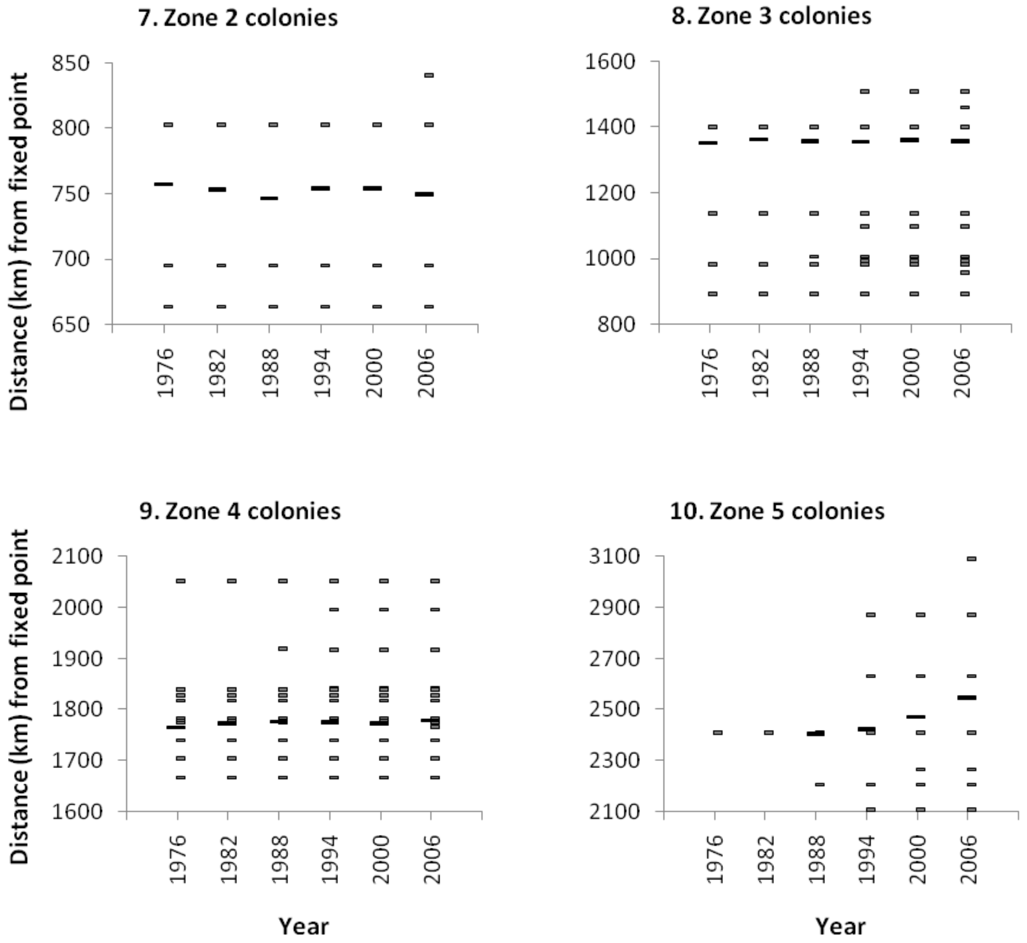


Figure 7 The location of Cape fur seal breeding colonies (small grey-filled markers) present in the population and various subsets of the population at six year intervals between 1976 and 2006, in terms of their distance from a fixed point (Woody Cape in Algoa bay, South Africa. The larger black markers represent the "centre of distribution" of the breeding population (or subset of the breeding population) per year, based on the application of equation 2 to the time series of predicted counts of each colony (determined using weighted 95th quantile regression analysis). The geographical distribution of zones 1–5 are shown in Figure 1 and breeding colonies within each of the subsets of the population are indicated in Table 1. Note the differences in scale of the y-axes between the panels.



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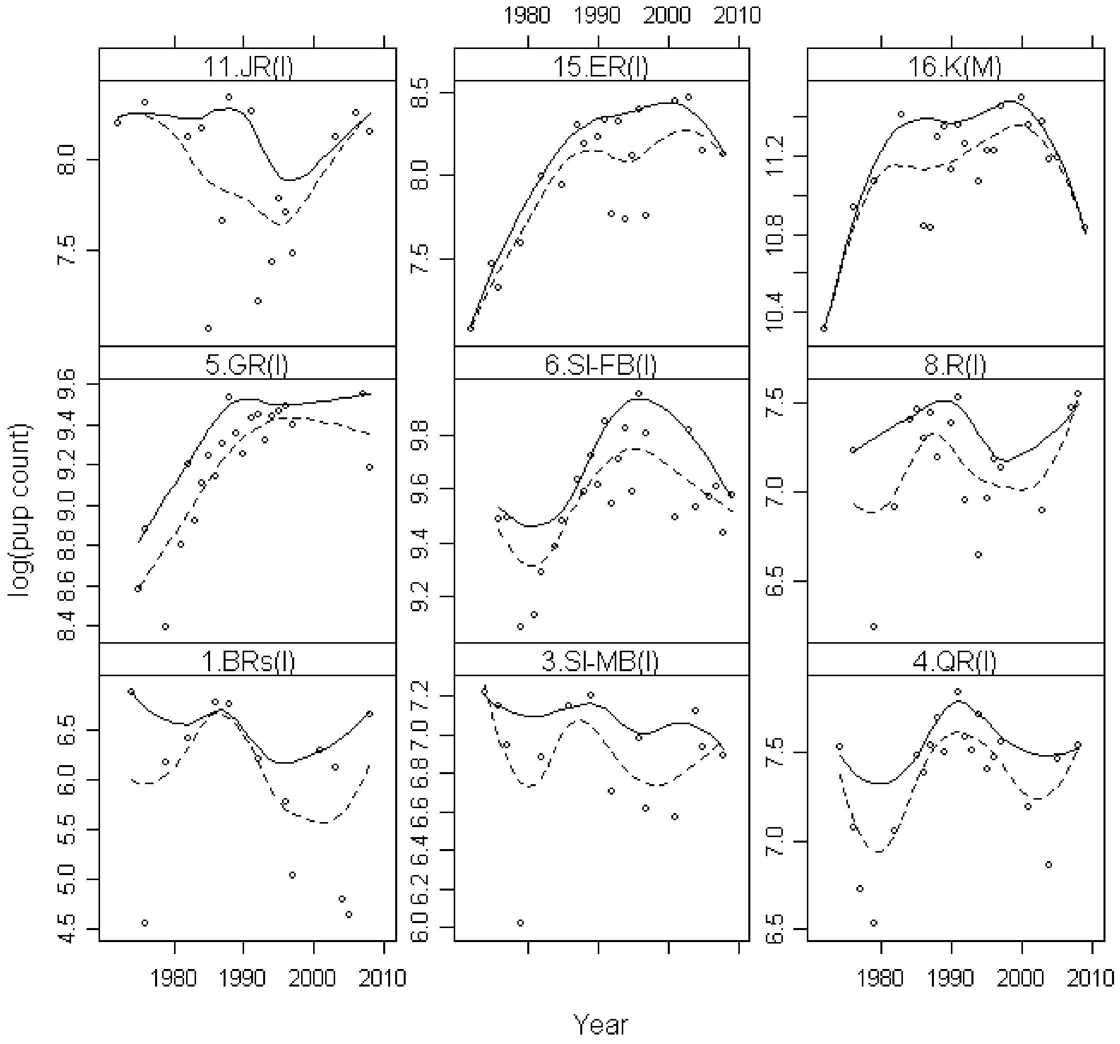
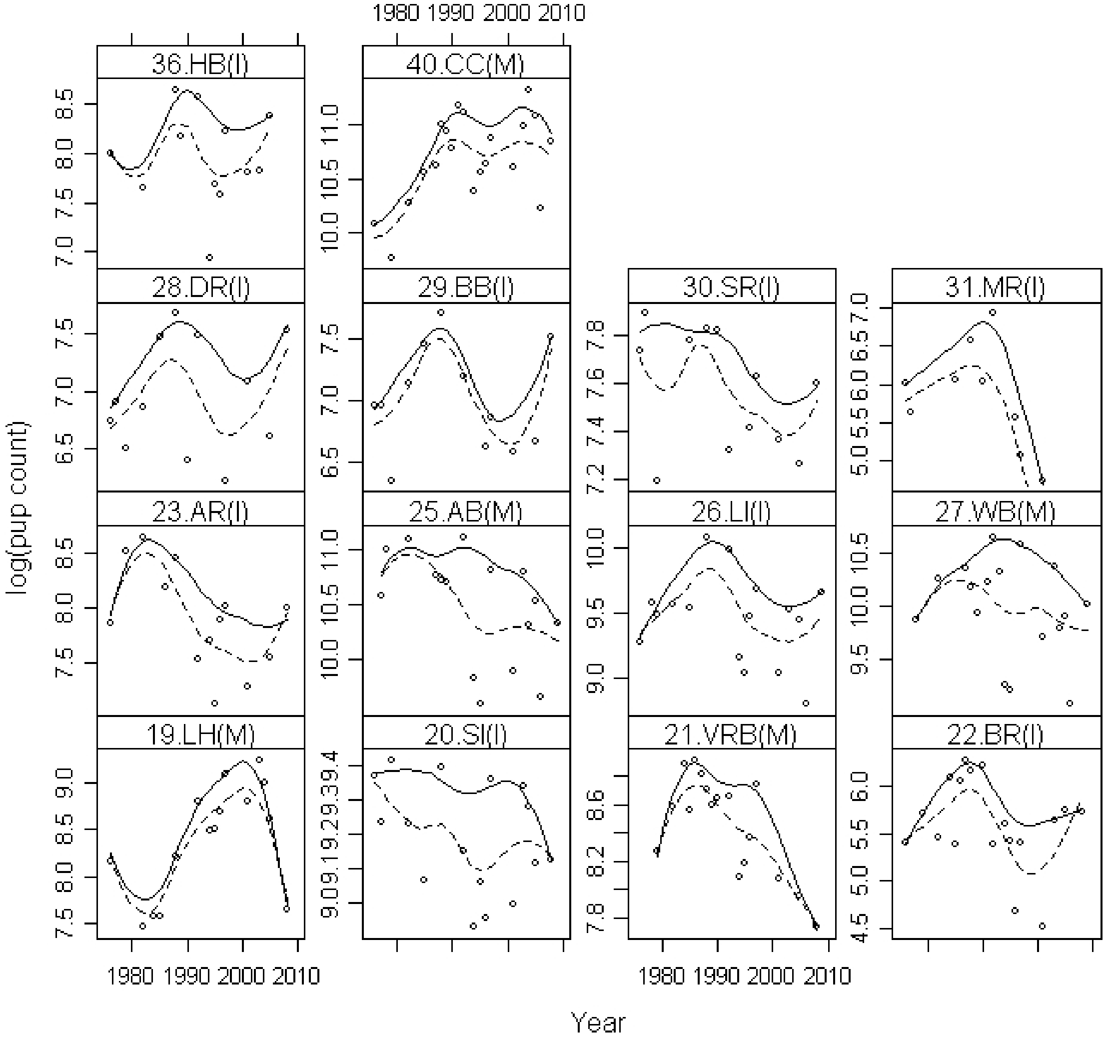
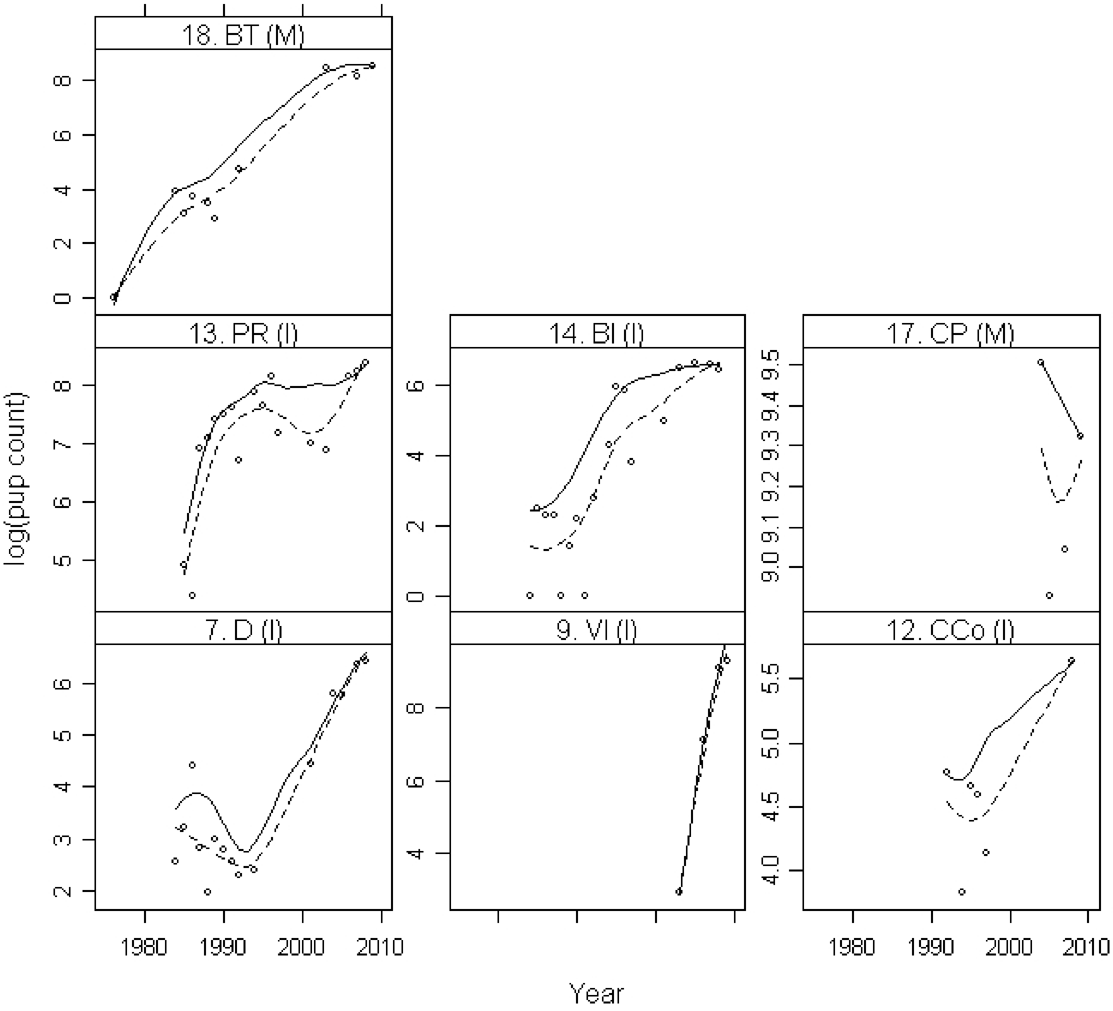
Appendix 1



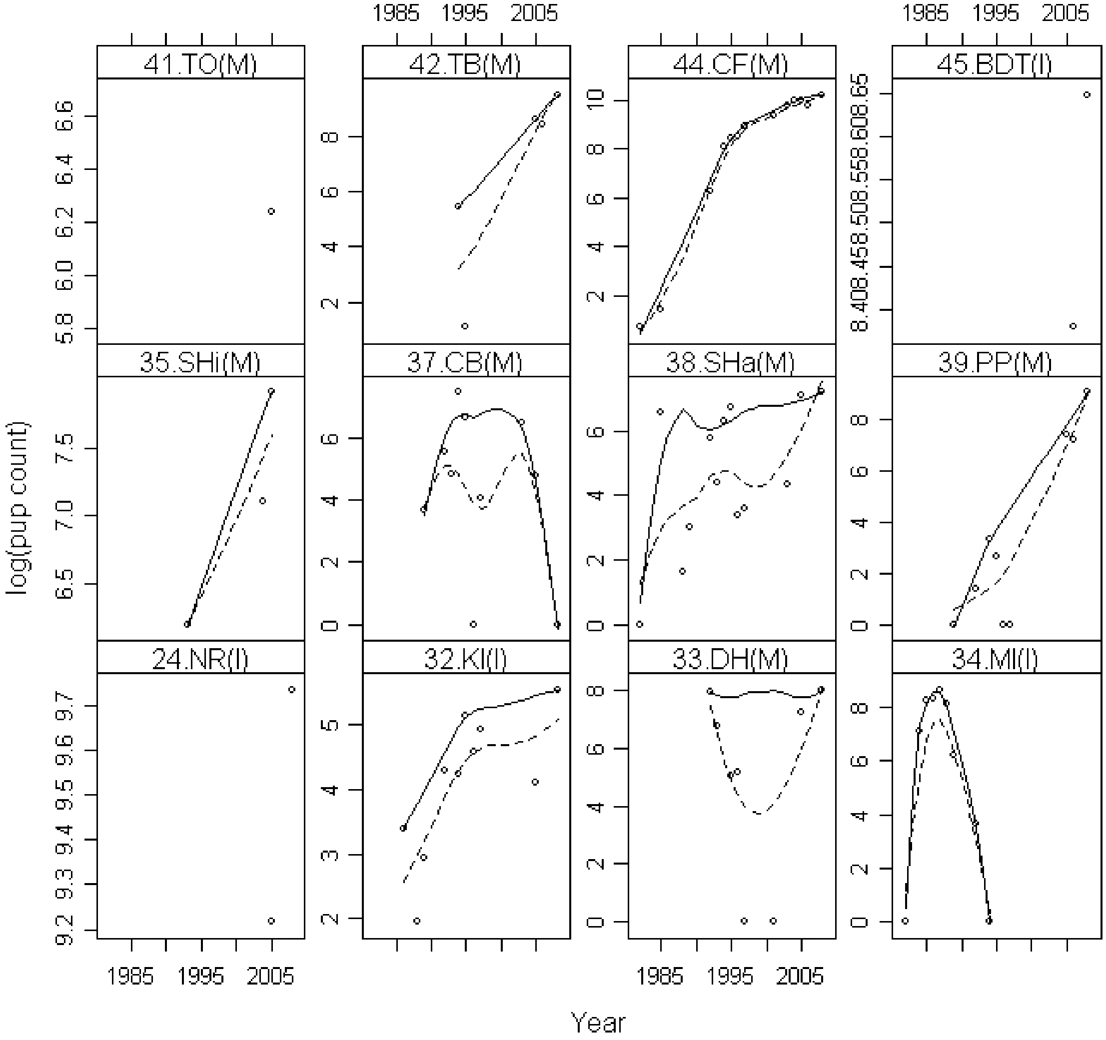
Appendix 1A Smoothed predicted curves fitted to raw counts (points) of Cape fur seal pups at South African breeding colonies that were in existence by 1971 (“existing” colonies), estimated using weighted 95th quantile (solid line) and least squares (dashed line) regression models. The number in the heading of each panel corresponds with the colony numbers in Table 1, and the “I” or “M” in parentheses refers to whether the colony is situated on an island or on the mainland. The abbreviated colony names represent the following: BRS = Black Rocks, SI-MB = Seal Island, Mossel Bay, QR = Quoin Rock, GR = Geyser Rock, SI-FB = Seal Island, False Bay, R = Robbesteen, JR = Jacob’s Reef, ER = Elephant Rock, K = Kleinsee.



Appendix 1B Smoothed predicted curves fitted to raw counts (points) of Cape fur seal pups at Namibian breeding colonies that were in existence by 1971 ("existing" colonies), estimated using weighted 95th quantile (solid line) and least squares (dashed line) regression models. The number in the heading of each panel corresponds with the colony numbers in Table 1, and the "I" or "M" in parentheses refers to whether the colony is situated on an island or on the mainland. The abbreviated colony names represent the following: LH = Lion's Head, SI = Sinclair Island, VRB = van Reenen Bay, BR = Black Rock, AR = Albatross Rock, AB = Atlas Bay, LI = Long Islands, WB = Wolf Bay, DR = Dumfudgeon Rock, BB = Boat Bay Rock, SR = Staple Rock, MR = Marshall Reef, HB = Hollam's Bird Island, CC = Cape Cross.



Appendix 1C Smoothed predicted curves fitted to raw counts (points) of Cape fur seal pups at South African breeding colonies that were established after 1971 ("additional" colonies), estimated using weighted 95th quantile (solid line) and least squares (dashed line) regression models. The number in the heading of each panel corresponds with the colony numbers in Table 1, and the "I" or "M" in parentheses refers to whether the colony is situated on an island or on the mainland. The abbreviated colony names represent the following: D = Duikerklip, VI = Vondeling Island, CCo = Cape Columbine, PR = Paternoster Rocks, BI = Bird Island, CP = Cliff Point, BT = Buchu Twins.



Appendix 1D Smoothed predicted curves fitted to raw counts (points) of Cape fur seal pups at Namibian and Angolan breeding colonies that were established after 1971 ("additional" colonies), estimated using weighted 95th quantile (solid line) and least squares (dashed line) regression models (colonies with two or less data points do not have curves fitted). The number in the heading of each panel corresponds with the colony numbers in Table 1, and the "I" or "M" in parentheses refers to whether the colony is situated on an island or on the mainland. The abbreviated colony names represent the following: NR = North Reef, KI = Klein Ichaboe, DH = Dolphin Head, MI = Mercury Island, SHi = Sylvia Hill, CB = Conception Bay, SHa = Sandwich Harbour, PP = Pelican Point, TO = Toscanini, TB = Torra Bay, CF = Cape Frio, BDT = Baia dos Tigros.

CHAPTER 7

An unusual nursing interaction between Cape fur seals

Abstract

Given the high costs of lactation and the importance of milk for pup growth and survival in pinnipeds, nursing behaviour directed by a lactating female towards another adult is unexpected. Here, details were noted of a nursing interaction that occurred between two Cape fur seal *Arctocephalus pusillus pusillus* adults. After discussing the event in the light of various hypotheses that have been put forward previously to explain uncharacteristic nursing behaviour in pinnipeds, a mother-son relationship between the interacting pair was considered to be the most likely explanation. The importance of being alert to rare and/or new behaviour in wildlife populations and of documenting such observations, given the current unprecedented rate of global environmental changes, was emphasised.

Keywords: adult, *Arctocephalus pusillus pusillus*, behaviour, interaction, lactation, nursing, South Africa

In nearly all pinniped species, mature females give birth annually, to a single offspring (pup) (Boyd 1991). Lactation may last for between four days and three years, depending on species (Sharp *et al.* 2006). Given the high costs of lactation (Oftedal 1993) and the importance of milk for the growth and survival of pups (Beauplet *et al.* 2003, Iverson *et al.* 1993), nursing behaviour directed by a lactating female towards another adult is unexpected. Here, I report on a nursing interaction which occurred between two Cape fur seal *Arctocephalus pusillus pusillus* adults. The event is discussed in light of various hypotheses that have been put forward previously to explain unusual nursing behaviour in pinnipeds.

On 30 July 2007, a large, sexually mature Cape fur seal male was seen feeding at the teats of a female considerably smaller than himself (see abbreviated video footage at http://sabap2.adu.org.za/docs/Seals_1.mov) at the Kleinsee breeding colony (29º34'S, 17º00'E) in the Northern Cape Province of South Africa. The male was observed to feed vigorously at all four of the female's teats and milk was visible at the teats. The female appeared to be tolerant of the male and even facilitated suckling. The pair was observed for approximately 1.5 hours, until nightfall. The male nursed from the female for most of this time, but occasionally interrupted feeding to challenge other males in the area or, in one instance, to investigate the observer. Following one such interruption, the female was laying ventrally so that her teats were inaccessible. On his return, the male nuzzled her side gently until she eventually raised one flipper and turned laterally to present her teats for him to resume feeding.

Additional behavioural data which may have provided clues as to the cause(s) of the interaction, such as whether the male also suckled (or attempted to suckle) from other females and whether or not the female had a pup of her own, could not be obtained. It was also not possible to obtain a genetic sample, therefore the relatedness of the interacting pair could not be determined. Based on the male's appearance and a comparison to other seals in video footage taken of the event, four experts independently estimated the age of the male to be at least eight years and his mass at least 180 kg. Eight is considered to be the minimum age at which Cape fur seal males are capable of securing breeding territories, even though puberty is attained four to five years earlier (Oosthuizen and Miller 2000). It was not possible to make a similar estimate of age for the female. The timing of the observation corresponds to the onset of the weaning phase, which for Cape fur seal pups of the year, occurs between 8–11 months after the season of births (November–December) (Rand 1955, 1967).

There are no other published records of adult-adult suckling interactions among Cape fur seals, and there are extremely few such records among other pinnipeds or other mammalian taxa. The only two published references of adult-adult suckling interactions among pinnipeds that were found both involved the Steller sea lion *Eumetopias jubatus* (Pitcher and Calkins 1981, Maniscolco *et al.* 2007). In nearly every published account of unusual nursing behaviour among pinnipeds, interactions between females and non-filial pups have been described. Most commonly, mistaken identity on the part of the female resulting from inexperience or confusion, or opportunistic milk theft, have been cited as the cause of such behaviour (e.g. Lunn 1992, Boness *et al.* 1992, Porter and Trites 2004, Maniscolco *et al.* 2007). However, such causes, which are consistent with the misdirected care hypothesis (Packer *et al*. 1992), do not seem applicable to the interaction described here. Firstly, the female was conscious of the male and tolerated his behaviour; secondly, it was extremely unlikely that the male could have been mistaken for a pup because of his large size – at the time of year of the observation, pups in the colony are only about 5–15 % of the male's estimated mass (unpubl. data). It was also unlikely that the female was intimidated into allowing the male to nurse from her, given that he did not behave aggressively towards her and she did not appear to be nervous of him. Therefore, it is necessary to consider the interaction not only in terms of fitness benefits for the male (gaining energy rich milk at little energy expenditure) but for the female as well. Two further hypotheses that are consistent with this condition were considered here, namely the need for the female to evacuate milk, and a mother-offspring relationship between the pair.

The need for a female to evacuate surplus milk at the end of an attendance period has previously been put forward as a theory to explain unusual nursing behaviour in some pinnipeds (Roulin 2002). However, it is probably not applicable to the situation described here. According to Roulin (2002), getting rid of milk that is surplus to the offspring's requirements before commencing a foraging trip, could serve to prevent teat infection in a pinniped female, or to reduce body weight and buoyancy to the benefit of swimming and diving ability, respectively. However, otariid (fur seal and sea lion) females do not have large milk storage organs and have the capability to modulate their lactation cycle in that they can produce milk rapidly “on demand” from their pup, then reduce milk production significantly in between suckling bouts (Sharp *et al.* 2006). It was therefore doubtful whether they would ever need to evacuate surplus milk; moreover, nursing another individual should have the counter-effect, of inducing further milk production.

It is generally assumed that the bond between pinniped mothers and their offspring is broken at weaning. However, persistence of recognition between a mother and her offspring after the latter has reached adulthood, is not unrealistic; – it has been demonstrated that mother-offspring pairs of the northern fur seal *Callorhinus ursinus* were capable of recognising each other’s vocalizations at least four years after the birth year, with little or no updating in between (Insley 2000). From that point of view, a mother-offspring relationship between the adult pair seems to be a more parsimonious theory than some form of reciprocity between unrelated individuals, for which there is no compelling evidence among pinnipeds (Trillmich 1996, Roulin 2002), or inclusive fitness benefits for the female derived from nursing non-filial kin (e.g. Gemmel 2003). However, this is speculative and needs to be tested by obtaining genetic samples if further observations of nursing interactions between adults are made.

Behaviour is the phenotypic component whereby individuals interact with their environment, and plasticity in behaviour in response to environmental changes may mediate effects of such changes. Considering the current unprecedented rate of global environmental changes (IPCC 2007), the importance of being attentive to rare and/or new behaviour in wildlife populations and of documenting such observations, must be emphasised.

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CHAPTER 8

Recommendations for a regional monitoring programme for Cape fur seals in the Benguela Current Ecosystem

Abstract

Marine top predators tend to be good indicators of alteration in trophic functioning and other ecosystem changes. The implementation of a regional monitoring programme for land-breeding top predators, including seals, is seen as integral to an ecosystem-based management approach to the living marine resources of the Benguela Current Ecosystem, especially considering the natural variability of the ecosystem, increasing fishing activity and global climate. Useful seal monitoring parameters and tools were discussed in the context of priorities that have been identified for an ecosystem monitoring programme in the Benguela Current Ecosystem. An integrated approach incorporating demographic, performance and behavioural attributes of seals was recommended. The need for co-ordinated monitoring effort and standardising of sampling techniques and data management software and procedures, was emphasised.

Keywords: *Arctocephalus pusillus pusillus*, Benguela, indicator, monitoring, recommendations, southern Africa, top predator

Background

In marine ecosystems, the distribution and abundance of living resources may be directly affected by changes in physical and oceanographic features (Beauplet *et al.* 2004). This is especially true in mid- and high-latitudes, where the annual seasonal cycle accounts for much of the total temporal variability in marine organisms (Bertram *et al.* 2001). While the general seasonal patterns repeat each year, climatic variability of the atmosphere and the ocean produce detectable changes in the timing and intensity of events (Bertram *et al.* 2001). Such variability can pose major challenges to the management of living marine resources, particularly since changes in marine ecosystems can be manifested in many different ways, on different temporal and spatial scales (Diamond and Devlin 2003). Moreover, in the last 150 years, increasing fishing activity and global climate change have been superimposed upon these natural environmental fluctuations (Hindell *et al.* 2003).

The Benguela Current Ecosystem that adjoins southern and western South Africa, Namibia and southern Angola, is an example of an ecosystem that experiences high levels of variability at different temporal and spatial scales (Shannon and Jarre-Teichmann 1999). It is characterised by high biological productivity, but experiences major fluctuations in the production of forage fish species, which has consequences for trophic functioning, fisheries, and socio-economic considerations (Shannon and Jarre-Teichmann 1999, Roux 2003), both within and across national boundaries. To ensure the sustainability of the ecosystem, management needs to take into account such variability, particularly considering the increasing threats of fishing and climate change. Thus, in order to sustain the health of the Benguela Current Ecosystem and guarantee the responsible use of its marine resources for current and future generations, all three countries in the region have committed an Ecosystem Approach to Fisheries (EAF) (Cochrane *et al.* 2004, Roux and Shannon 2004). EAF differs from conventional management approaches (e.g. the single species approach) in that it considers the cumulative effects of different ecosystem components and aims at understanding the connections and key processes between them, ultimately with the goal of maintaining the ecosystem in healthy and productive state so that it can provide goods and services that human populations depend upon.

As they are sensitive to changes in the abundance and distribution of their prey species (Crawford *et al.* 1983, Weimerskirch *et al.* 2003), marine top predators tend to be good indicators of alteration in trophic functioning and other ecosystem changes (Diamond and Devlin 2003, Reid *et al.* 2005). Therefore, these predators are increasingly being used to monitor variability in marine ecosystems (Montevecchi and Myers 1995, Boyd and Murray 2001). Terrestrial breeding marine top predators are potentially most useful in this regard. This is because their relative accessibility when on land facilitates the monitoring of their reproductive performance, their population trends and aspects of their foraging ecology, all of which may be affected by the distribution and abundance of prey species.

The most prominent mammalian land breeding marine top predator in the Benguela Current Ecosystem is the Cape fur seal *Arctocephalus pusillus pusillus* (Wickens *et al*. 1992a). Historically, the breeding distribution of this species ranged from the south-east coast of South Africa to central Namibia (Rand 1972, Shaughnessy 1984). Over the last 40 years there has been a northward shift in the distribution of the population, with a colony recently establishing as far north as Baia dos Tigros, southern Angola (Chapter 6). Management priorities for Cape fur seals vary between countries in the Benguela Current Ecosystem. In South Africa, seals are utilised as a non-consumptive resource (ecotourism) and may not be killed for profit (DEAT 2007), whereas in Namibia, seals are harvested annually for commercial profit according to a quota system (Roux and Sakko 1997). However, notwithstanding different management objectives within the region regarding the seal population, the implementation of a regional monitoring effort for land-breeding top predators, including seals, is integral to an ecosystem-based management approach to the living marine resources of the region.

Considerations for region-wide monitoring

Based on the management objectives within the region and on relevant international declarations, some priorities for an ecosystem monitoring programme in the Benguela Current Ecosystem using land-breeding top predators have been proposed (BCLME Top Predators Steering Committee 2007). These are listed below (*a-f*) and discussed with regard to which monitoring tools should be used to achieve these objectives in the case of the Cape fur seal.

(a) *Monitoring the conservation status of top predator species of conservation concern, and assessing and updating their conservation status*

Although the conservations status of the Cape fur seal is regarded as "least concern", several potential threats to the population have been identified (Kemper *et al.* 2007). These include prey shortages due to environmental fluctuations or over-fishing, ongoing harvesting/culling in Namibia, and mortality related to fishing operations (incidental and intentional). Because counts of pups may be used as an indication of population size (Wickens and Shelton 1992), continuation of the frequent censuses of breeding colonies, which occurred between 1971 and the present (Chapter 6), will allow for any changes in abundance to be monitored. In addition, incidence of seal mortality in fishing operations, such as drowning in trawl nets (Wickens *et al.* 1992a) should be monitored.

(b) *Providing indices of the state of health of marine ecosystems using top predators*

Parameters to measure for providing indicators should be responsive to environmental variability. Hindell *et al.* (2003) broadly classified possible monitoring parameters into the following three groups: (i) Demographic attributes (e.g. changes in abundance and distribution of population); (ii) Performance attributes (e.g. reproductive output or success); (iii) Behavioural attributes (e.g. diet, foraging patterns). A key to using predators as indicators of the state of ecosystems is understanding of relationships between predators and appropriate biological (e.g. prey abundance estimates from censuses) or physical (e.g. upwelling indices) parameters (Croxall *et al.* 1999). Long term monitoring of such parameters needs to be in place for meaningful indices to be created from time series of information on predators.

Censuses of pups permit detection of medium to long term trends in the abundance and distribution of the breeding population (demographic attributes), which may be related to ecosystem changes (including prey shifts), density dependence, or anthropogenic effects. Considering the changes documented in the distribution and abundance of prey species (e.g. Crawford *et al.* 2008), emphasis should be placed on searches for new haulout colonies in remote areas, and confirming the formation of new breeding colonies where suspected (e.g. Chapter 6).

Apart from an index of population trends, pup counts can be seen as a measure of reproductive output (performance attribute) interpretable at a finer time scale, since they may fluctuate between years due the effects of environmental variability on birth rates (Wickens and Shelton 1992, Chapters 2 and 5). However, for logistical reasons, obtaining comprehensive coverage of the entire population on an annual basis may not be practicable. Furthermore, excepting for extreme events, it is generally difficult to establish a causal link between changes in numbers and a specific environmental change (Hindell *et al.* 2003). Therefore, censuses as indicators of ecosystem effects on the seal population are not sufficient on their own, and other attributes should be monitored in conjunction with abundance.

Other performance attributes that are amenable to monitoring include the annual average growth rate (or some index thereof) or indices of pup condition (e.g. mass) at any specific period, such as at the time of weaning. These parameters, which could have direct consequences for pup survival (and consequently reproductive success of adult females), reflect the rate of energy transfer from females to their pup and therefore provide a good indication of prey availability (Reid 2002, Beauplet *et al.* 2004). Indeed, strong correlations have been found between coastal upwelling indices at Lüderitz, the main upwelling centre in the Benguela Current Ecosystem, and the average growth rate/weaning mass of pups in the region (Roux 2002). Thus, pup growth parameters may serve as an index of environmental variability and prey availability (Peard 2007). Because adult female fur seals are central place foragers during the lactation period, these parameters can be expected to reflect conditions whose spatial and temporal boundaries can be readily determined or estimated (Reid 2002). However, unlike some other local top predators such as the African penguin *Spheniscus demersus*, Cape fur seals are generalist feeders and are able to switch prey and possibly maintain their overall energy intake when the abundance of a prey resource declines (Chapter 2). Therefore, neither their performance nor their demographic attributes are likely to be reliable indicators of any particular prey species, and these parameters should ideally be supplemented with other information, such as diet (behavioural attribute).

The diet of seals can be monitoring using a cheap and practical method such as analysis of scats collected in colonies, which can provide important information on spatial and temporal changes in diet (Tollit and Thompson 1996) (but see Annex 1, section 4.6.1 for potential shortcomings of this approach). With regard both to the monitoring of diet and of performance attributes such as pup growth/weaning mass, it is important that studies be designed with adequate replication to address the high levels of spatial and temporal variability that occurs throughout the seals' range in the Benguela Current Ecosystem. Furthermore, considering the substantial individual variation that may occur within performance and behavioural parameters, large sample sizes should be aimed at (Hindell *et al.* 2003). In practice, these ideals may not always be achievable considering the inaccessibility and difficult working conditions that characterise many seal colonies. Indeed, the need for large sample sizes and spatio-temporal replication tend to compromise the feasibility of region-wide monitoring certain parameters for providing indices of ecosystem health. This possibly includes the monitoring of annual pup survival rates and the timing of breeding, both of which may vary according to inter-annual variability in food availability (Bertram *et al*. 2001, Beauplet *et al*. 2005) but which require intensive effort.

The development of modern instruments (e.g. satellite transmitters, time-depth recorders) that can be deployed on seals during shore visits, allow for investigation of geographical and vertical variation in foraging effort or behaviour (behavioural attribute), and may provide clues regarding changes in prey availability (e.g. Guinet *et al.* 2001). Such instruments are expensive and considering the desirability of replication and representative sample sizes may not be practicable as routine monitoring tools. However, information obtained from such studies may serve to facilitate understanding of relationships between monitored parameters of the predators and prey availability or environmental variability. Furthermore, performance and demographic responses to physical changes in the environment that affect feeding conditions would be lagged, except perhaps in extreme circumstances, whereas behavioural responses can be expected to occur soon after such events. The ability to detect behavioural responses to ecosystem changes, for example by using telemetry, has obvious advantages in terms of providing early warning or confirmation of events.

(c) *Accounting for the requirements of top predators dependent on species targeted by fisheries*

Censuses of pup numbers, together with information on relevant life history parameters (e.g. standing age distribution, survival, fecundity, age at first breeding and longevity) can be used to model population size and trends (e.g. Wickens *et al.* 1992b). This, with information on diet (e.g. from scats), energy requirements, calorific content and digestibility of prey, can be used to estimate the prey requirements of the seal population or components thereof (e.g. Mecenero *et al.* 2006). Information on prey consumption of the seal population can be included in ecosystem models to investigate trophic relationships between seals and other top predators, as well as commercial fisheries (e.g. Roux and Shannon 2004).

(d) *Providing information useful in the management of prey resources, based on top predators*

Diet data derived from seals may complement conventional fisheries science in providing quantitative information relevant to management considerations for commercial fisheries, e.g. age estimation, forecasting recruitment. Sampling and analysis of seal scats from key colonies has been shown to be an appropriate technique for providing such information (Roux 2007, Mecenero *et al.* 2007).

(e) *Managing interactions between species of top predators, where one or more species are of conservation concern*

Continuation of the census time series is relevant for identifying potential areas of concern with regard to species interactions, such as between seals and threatened seabird species (e.g. Makhado *et al.* 2006). For example, local increases in seal numbers in the vicinity of important seabird breeding habitat may be detected in its early stage through regular censusing, allowing for timely intervention by management authorities if preservation of the seabird colonies is seen as a priority.

(f) *Assessing the outcomes of conservation interventions*

Continuation of the census time series may also be relevant to monitoring the outcomes of management interventions. An example is monitoring the effects of displacement of seals from the vicinity of seabird breeding habitat (Chapter 3), including re-location to new sites. Scat sampling can allow for monitoring of predation levels of seals on seabirds, using the frequency of occurrence of seabird remains in seal scats (Mecenero *et al*. 2005, Kirkman *et al*. 2000).

Recommendations for a region-wide monitoring programme

In summary, the following recommendations are made for the monitoring of seals in the Benguela Current Ecosystem:

- An integrated approach should be followed, incorporating demographic, performance and behavioural attributes of the seals. As a minimum the programme should aim to monitor at least one parameter relevant to each of these attributes. Based on their applicability to the various management objectives and their practicability, the following three parameters are suggested as minimum requirements: pup production (aerial censuses), an index of pup growth rate/weaning mass, and diet;
- The monitoring studies should be carefully designed with the various scales of spatial and temporal variability in mind. Emphasis should be placed on the need for suitable sample sizes considering the substantial individual variation that may occur within performance and behavioural parameters;
- Assessments of historical information, where available, should be conducted to facilitate the estimation of desirable levels of spatial and temporal coverage and sample sizes;
- Wherever possible, monitoring studies should be co-ordinated between researchers and/or areas, i.e. with regard to which parameters are monitored and the timing of sampling, to facilitate comparison;
- Sampling/data collection techniques should be standardised between regions and over time. Detailed explanations of various basic monitoring techniques, including those applicable to the studies of diet, pup growth and abundance, are provided in Annex 1 of this thesis;
- Standardising data management software and procedures will facilitate the sharing of information between regions;
- In order to assess the usefulness of parameters as indicators of ecosystem health and to allow meaningful interpretation of variability in results, the time series of information collected need to be linked to other physical or biological parameters relevant to prey availability;

- Research using sophisticated technological devices such as satellite transmitters or time-depth recorders to investigate foraging effort/behaviour of seals should be encouraged. Such studies can facilitate understanding of relationships between measured parameters of the predators and prey availability or environmental variability;
- Although it is desirable to keep up with technological and scientific advances, the introduction of new techniques should not jeopardise existing monitoring programmes; the development of reliable long term time series of information depends upon continuity. Where it is desirable to overhaul a monitoring technique (e.g. replacement of black-and-white film with digital photography for aerial censuses), emphasis should be placed on calibrating the results of the old and the new techniques, before the old is discarded.

Based on the above and the methods described in Annex 1 of this thesis, suggestions for a seal monitoring programme in the Benguela Current Ecosystem are presented in Tables 1–3. Three different levels of monitoring intensity are considered, based on a hypothetical scale of increasing financial support and regional co-operation. (i) “Basic” refers to the minimum monitoring requirements to provide essential data for long term management, and involves routine monitoring; (ii) “Desirable” is the suggested short to medium term goal for a regional monitoring initiative, in terms of monitoring effort; (iii) “Optimal” assumes the existence of a substantially funded, dedicated regional team.

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Table 1 Recommended “basic” Cape fur seal monitoring programme for the Benguela Current Ecosystem.

Parameter	Technique	Spatial resolution	Temporal resolution
Pup numbers	Aerial census	Entire range	1 in 3 years
Index of pup condition at 6 weeks after birth	X-samples of pup mass	Representative colonies in SA and Na. (e.g. 3 each)	1 sample per year at a specified date
Index of pup condition at weaning	X-samples of pup mass	Representative colonies in SA and Na. (e.g. 3 each)	1 sample per year at a specified date
Diet	Scat sampling	Representative colonies in SA and Na. (e.g. 4 each), Baia dos Tigros (An.)	Monthly for SA and Na., seasonally in An.
	Scat sampling	Selected colonies	More frequent scat sampling (e.g. bi-monthly) if necessary for fish monitoring studies (e.g. ageing)

(SA = South Africa, Na. = Namibia, An. = Angola, X-sample = cross sample)

Table 2 “Desirable” Cape fur seal monitoring programme recommended for the Benguela Current Ecosystem (additional to activities listed in Table 1).

Parameter	Technique	Spatial resolution	Temporal resolution
Pup numbers	Aerial census	Selected colonies/regions (e.g. harvested colonies, local populations declining or growing rapidly)	More frequent censuses, e.g. annually
	Aerial census	Entire range	Additional censuses in the case of major environmental events, mass mortality event or mass abortion events
Index of pup growth	X-samples of pup mass	Representative colonies in SA and Na.	Monthly sampling, Jan-Sep
Diet	Stable isotope measures	Colonies representative of regional diet (based on scats)	Seasonal

(SA = South Africa, Na. = Namibia, An. = Angola, X-sample = cross sample)

Table 3 “Optimal” Cape fur seal monitoring programme recommended for the Benguela Current Ecosystem (additional to activities listed in Tables 1 and 2).

Parameter	Technique	Spatial resolution	Temporal resolution
Pup numbers	Aerial census	Entire range	More frequent censuses, e.g. annually
Pup size at birth	Weighing of pups at birth	Representative colonies in SA and Na.	Annual
Measures of pup growth	Longitudinal sampling	Selected colonies	Annually for specified period (e.g. from birth to 60 days of age)
Trip duration	VHF monitoring	Selected colonies	Annually for specified period
Foraging range, at-sea movements	Satellite telemetry	Selected colonies	Annually for specified period
1st year survival estimates	Tagging of pups and subsequent monitoring	Selected colonies	Annually
Breeding phenology	Pup counts to monitor timing of birth	At least 3–4 colonies selected to be representative of range	Annually

(SA = South Africa, Na. = Namibia, An. = Angola, X-sample = cross sample)

CHAPTER 9

Synthesis

Cape fur seals *Arctocephalus pusillus pusillus* occur along the southern and western coasts of southern Africa, where they currently breed at numerous island and mainland locations (Chapter 6). The range of the seal population largely coincides with the Benguela Current Ecosystem, which is characterised by substantial upwelling induced productivity (Bakun 1996). This productivity of the marine environment together with cool climatic conditions and the availability of suitable breeding areas, provide conditions suitable for the seal population to prosper (Shaughnessy 1984, van der Lingen *et al*. 2006, Peard 2007). However, the Benguela Current Ecosystem is also characteristically variable at different spatial and temporal scales (Shannon *et al.* 1988, Shannon and Jarre-Teichmann 1999); changeability in its productivity can have considerable consequences for prey and predator populations, as well as for human livelihoods. The variability of the ecosystem and the transboundary occurrence of several commercial fishery stocks and top predator populations that they sustain, are some of the challenges to the successful management of the marine and coastal environment of the region. Especially in the past decade, there has been increasing recognition of the importance of ecosystem-based management, including an Ecosystem Approach to Fisheries (EAF) and transboundary co-operation with regard to research, monitoring and management, for addressing these issues in the region (Cochrane *et al*. 2004). Concurrent with the growth of EAF, there has also been increasing recognition that monitoring information on top predators in the marine ecosystem can provide useful indicators of *inter alia* ecosystem health, changes in marine resources and trophic interactions that have direct or indirect impacts on human livelihoods, all of which are informative for EAF (Boyd and Murray 2001, Reid *et al*. 2005, Kirkman 2007).

This thesis had its origin in the Benguela Current Large Marine Ecosystem (BCLME) Programme’s project “Top Predators as Biological Indicators of Ecosystem Change in the BCLME” (LMR/EAF/03/02) (Kirkman 2007). Implicit in the objectives of this project were (*inter alia*) the review and analysis of existing time series of information on land-breeding top predators in the region, assessment of linkages between the time series and comparative information (giving consideration to means of mitigating adverse influences), defining of objectives for an ecosystem monitoring programme based on top predators and identification of parameters required to attain these objectives, testing and description of appropriate methods for monitoring and the formulation of recommendations for an integrated ecosystem monitoring programme based on land-breeding top predators.

Directly or indirectly, this thesis was in line with attaining these objectives, specifically by (a) Analysing existing time series of information on seals (Chapter 2, 4, 5 and 6); (b) Describing changes in the distribution and abundance of the seal population and providing insight into intrinsic and extrinsic factors potentially underlying these changes (Chapters 2, 5 and 6); (c) Giving consideration to management implications of the observed changes in the seal population, including mitigation of detrimental effects on other species (Chapters 3 and 6); (d) Contrasting the results of alternative approaches for analysing time series of information (Chapters 2 and 6); (e) Assessing detrimental effects of certain research on seals and implications for the interpretation of data (Chapter 4); (f) Testing satellite transmitters for use in an ecosystem monitoring programme (Chapter 5); (g) Providing recommendations for seal monitoring taking into account monitoring priorities that have been identified for the region and differences in capacity for seal monitoring within the region (Chapters 2, 4, 6, 7 and 8); (h) Detailing appropriate techniques for seal monitoring taking into account the large size and widespread distribution of the population, variability in the monitored parameters and the welfare of study animals (Annex 1); (i) Proposing research of relevance to the enhancement of monitoring protocols and ensuring correct interpretation of monitoring outcomes (Chapter 4, Annex 1).

The time series of information that received the greatest focus in this thesis was the aerial photographic census time series of seal pups at breeding colonies, which commenced in 1971. This was the longest available time series and the only one that was representative of the entire geographical range of the population. Potential weaknesses of the approach were acknowledged and were discussed in Annex 1 (Section 2.6). Despite these weaknesses, pup counts are considered to provide the best available index of changes in pup production between years (Shaughnessy 1987) and of the total population size of seals (Wickens and Shelton 1992). In addressing the issue of missing data in this time series and effects thereof on its analysis and interpretation, results of different models for approximating missing data values for breeding colonies made it apparent that there were area-specific differences in numerical patterns over time (Chapter 2). Breeding colonies in Namibia, which largely coincide with the northern component of the Benguela Current Ecosystem and where approximately 60% of the seal population occurs, tended to fluctuate considerably between years especially in the latter part of the time series (1992–2003), with coherence in the trends between colonies. Pup counts are reflective of both the size of the breeding-age populations and birth rates, but because the size of the former cannot fluctuate between years with the magnitude of the observed fluctuations in pup counts, it could be assumed that variability in birth rates was largely accountable for these fluctuations. This was supported by the high incidence of abortions noted at Namibian colonies in certain years characterised by environmental perturbations (Roux 1998, 2002). Considering the coherence in the numerical patterns over time between colonies in the south of Namibia, including colonies that were subjected to sealing during the last 20 years and those that were not, it was evident that a determinant operating at a wide spatial scale, such as effects of environmental variability on prey availability, was mainly accountable for the observed patterns. This was realistic because it is known that birth rates of seals can be negatively impacted upon by prey shortages (Guinet *et al.* 1998) and also because widespread starvation of seals including pups but also adults, occurred during years with anomalous environmental conditions.

On the other hand, breeding colonies in South Africa, which largely coincide with the southern component of the Benguela Current Ecosystem, were characterised by less variability in numbers between years and little coherence in the numerical trends between breeding colonies. It was concluded that the distinct numerical patterns between the northern and southern Benguela Current Ecosystems reflected differences in the state of the marine environment between the two areas, especially after the early 1990s. Since then, the northern Benguela Current Ecosystem has been characterised by wide-scale environmental perturbations that induced severe periodic prey shortages and re-distribution of prey stocks, a situation that was probably exacerbated by over-fishing (Gammelsrød *et al*. 1998, Boyer and Hampton 2001, Cury and Shannon 2004). In contrast, the southern Benguela Current Ecosystem was characterised by a relatively stable environment and conservative management of fish stocks (van der Lingen *et al*. 2006). From the lack of coherence in the numerical trends between colonies in South Africa, at least during the time series considered in Chapter 2, it is possible that the most important determinant(s) of numerical growth for this component of the population may have operated at more localised spatial scales, perhaps typical of localised density dependence or effects of storms on breeding colonies or a combination of these.

An increase in the number of breeding colonies in the population of c. 43 % occurred during the study period. The majority of the new colonies were situated on the mainland, mostly in central and northern Namibia but also along the west coast of South Africa and one new breeding colony was established in southern Angola, the latter representing a northward range extension of the seal breeding population (Chapter 6). Furthermore, analysis of the time series of pup counts per breeding colony (including newly established colonies) with consideration of the distance of each colony from the eastern-most extreme of the range, showed a significant northward shift in the centre of the distribution of the breeding population. Despite these changes, analysis of the pup count time series indicated that the size of the seal population in the last decade was similar to its size in 1992, the time of the last comprehensive assessment of the population's size, which was estimated at approximately 1.7 million animals (excluding pups) (Butterworth *et al*. 1995).

The numerical trends of the seal population, including its recovery from past over-exploitation (including prior to the study period) and recent trends (during the study period) were considered in the light of theory on fur seal re-colonisation (Chapter 6). The persistence of the seal population at the time when legal controls on sealing were introduced (early 20th century) and its subsequent recovery during the 20th century, including re-colonisation of some of its former habitat and colonisation of new areas, appeared to be consistent with the first three phases of Roux's (1987) paradigm on fur seal re-colonisation, namely "survival", "establishment" and "re-colonisation". However, despite that the modelled trends in total pup numbers levelled off after the early 1990s (Chapter 6), the pronounced variability of pup counts in this period especially at colonies in the south of Namibia, the decline of several breeding colonies in the same area during this period and the establishment and rapid growth of several new breeding colonies in central and northern Namibia and southern Angola, did not appear to be consistent with the onset of an equilibrium or "maturity" phase, as in Roux's (1987) paradigm.

While Roux's (1987) model has been shown to be applicable to the patterns of expansion of other otariid populations recovering from over-exploitation (Hofmeyr *et al*. 2006, Bradshaw *et al*. 2000, Grandi *et al*. 2008), these were populations that were situated on oceanic islands or on mainland peninsulas and were therefore localised relative to the Cape fur seal population's extended range. During its re-colonisation phase, the Cape fur seal population has evidently been exposed to several pressures other than density-related limitations, which have varied throughout its range and contributed to the dynamic state of the population post-1992, in terms of its distribution and abundance. One of these, discussed above, is the unpredictability of the ecosystem. The importance of ecosystem variability as a density independent influence on the population dynamics of seals has been emphasized by several authors (e.g. Trillmich 1993, Matthee *et al.* 2005, Reid and Forcada 2005). Adult female fur seals (on which the burden of parental care wholly rests) are central place foragers that must locate prey within a limited geographic range of their breeding colony to reproduce successfully (Lea *et al.* 2006). Therefore extrinsic effects that cause shortages of prey within this range can conceivably influence dispersal to new environments. The fact that the direction of the distributional shift of the breeding population in the northern Benguela Current Ecosystem corresponded with the direction of the shifts in prey availability in this component of the ecosystem (Boyer and Hampton 2001, Axelsen *et al.* 2004, van der Lingen *et al.* 2006), supported the theory that prey limitation related to unfavourable environmental conditions (Peard 2007) and possibly also over-fishing (Boyer and Hampton 2001) played an important role in these changes.

This was further supported by the results of Chapter 5, where satellite-tagged study seals from the south of Namibia displayed behaviour that was interpreted to indicate poor feeding conditions in this area, including long foraging trips, low fidelity to their tagging colony and to foraging areas, and displacement to other colonies. Almost invariably, the direction of foraging trips and displacement was northward, congruent with the shift in the breeding population's distribution (Chapter 6) and the known shifts in prey availability. In contrast, study seals from northern Namibia generally displayed fidelity both to their colony and to foraging areas, suggesting reliable prey resources. The results of the study were interpreted to reflect a general gradient of improving feeding conditions from south to north in the northern Benguela Current Ecosystem, which was consistent with the known distribution of prey in the area after the depletion of prey stocks in the south caused by environmental changes and fishing, and the northward re-distribution of certain prey stocks (Boyer and Hampton 2001, Axelsen *et al*. 2004, van der Lingen *et al*. 2006). The results were also interpreted to reflect the adaptability of the Cape fur seal to the unpredictable environment through flexible use of foraging and breeding space. This may be the key to the persistence of the population at its current level, despite adverse environmental conditions and human pressures (sealing, fishing) over much of its range.

Another difference between the Cape fur seal population and other otariid populations for which recovery in numbers following over-exploitation has been described is that sealing of Cape fur seals continued during the population's recovery (Kirkman and Lavigne 2010), under legal control for the past century (Shaughnessy 1984). In Chapter 4, it was shown that intensive research-related disturbance in localised study sites within a breeding colony resulted in breeding animals dispersing away from the disturbed sites of the colony, which were subsequently characterised by low levels of density in succeeding years. It was a reasonable assumption that this effect was symptomatic of stress caused by research activities, which was consistent with the theory that intense, repetitive human disturbance of animals that associate humans with predation risk should result in a shifting of habitat (Frid and Dill 2002). Like the investigator disturbance described in Chapter 4, disturbance caused by sealing activities is chronic in that it is repeated daily in colonies for an extended period of time. However, effects of sealing operations on breeding colonies are more extensive in that they are conducted at the scale of entire colonies and entail greater levels of disturbance than the research activities, which were conducted with caution to avoid negative impacts upon the welfare of study animals (e.g. injury or distress) that could indirectly influence research findings.

It follows that disturbance associated with annual sealing activities at the scale of entire colonies could conceivably have caused dispersion of breeding animals to other locations, where they may have contributed to the establishment and growth of new breeding colonies. Indeed, Gentry (1998) demonstrated that despite inherent site fidelity, breeding fur seal females are flexible enough to re-locate under conditions of human disturbance, as long as there is a group of conspecific animals to disperse to. In Namibia, the latter stimulus was available at several colonies in the north and centre of the country that were previously classified to be non-breeding colonies by Oosthuizen and David (1988), but which developed into breeding colonies during the study period. Therefore, it is a reasonable hypothesis that sealing, even at sustainable levels in terms of the number of seals taken, could have played a role in the development and growth of new breeding colonies during the study period, as a result of disturbance at those breeding colonies subjected to sealing activities. Since 1990 when sealing was discontinued in South Africa, this pressure has been limited to Namibia, which is also where most of the new breeding colonies developed after 1990.

On the whole, it is difficult to separate the effects of the environment, human interference and density dependence on the observed patterns in distribution and abundance of the population, with the data that is available, and it is likely that combinations of these factors have played a role in the spatio-temporal dynamics of the seal population observed during the study period. To improve understanding of the drivers of seal population dynamics, including being able to distinguish between human- and climate-related effects on trends in population abundance and distribution, region-wide monitoring of other population parameters to complement continued aerial census monitoring, was recommended (Chapters 6 and 8). These included key performance (e.g. growth) and behavioural (e.g. foraging ecology) attributes of seals that can be related to environmental or other biological variables. Region-wide monitoring of various key aspects of the seal population is also of relevance to ecosystem-based management of marine resources in the Benguela Current Ecosystem, including effects of seal population dynamics on human livelihoods and the conservation of other top predators in the region. The need for a holistic approach to monitoring and management of top predator populations was illustrated in Chapter 3, where it was argued that in the past, researchers may have been distracted from wider consideration of potential detrimental effects on the conservation status of locally breeding seabird populations by the conspicuousness of predatory seals and certain of their behavioural tendencies.

Of the three main management issues that concern the Cape fur seal, i.e. commercial sealing, seal-fishery interactions and seal-seabird interactions, only the latter received particular attention in this thesis (Chapter 3). Monitoring and managing the direct impacts of seals on endemic seabird populations with unfavourable conservation status is relevant to ecosystem-based management and was one of the monitoring priorities identified for the region (Chapter 8). Various theories for the perceived increase in seal-seabird predation since the 1980s were considered in Chapter 3. While none of the theories could be disproved, the facts that predatory attacks were generally limited to a certain sex-age component of the population (subadult males) and that seals apparently learn to prey on seabirds through play and through observing other seals when hunting were considered to be of greatest relevance to the management of this interaction. Based on this model of behavioural development and spread, incidence of seal-predation could proliferate irrespective of overall trends in seal numbers, therefore non-selective control of seal numbers may not have the desired effect of reducing predation on seabirds, especially as indiscriminate culling may not eliminate the problem animals (Lavigne 2003). Arguments propounding a general reduction of seal numbers for the benefit of seabird conservation or fisheries management, on the basis that the present population size exceeds the pre-sealing level, were evaluated and found to be unjustified.

Apart from recommendations for a regional monitoring programme (Chapter 8) and how to implement it (Annex 1), further research requirements with regard to the strengthening of monitoring protocols stem from this thesis. These include calibrating for the effects of technological advances in equipment and techniques on the aerial photographic census time series, and investigating inter-annual and geographical differences in breeding phenology and potential effects of this on comparisons of aerial census results (Annex 1). Furthermore, given the recent technological advances in telemetric instrumentation, the question of the pervasiveness of scavenging around fishing boats in the seal population (David 1987, Wickens et al 1992, see Chapter 3) could be re-addressed, perhaps using sophisticated devices such as GPS/camera loggers to explore interactions with fishing fleets at an individual level. Telemetry also provides the possibility of attempting experimentally to distinguish effects of human interference from other effects on seal behaviour, including foraging behaviour and fidelity to breeding and feeding sites (Chapter 5), by deploying instruments on animals in a colony subjected to sealing and as a control, in a nearby colony that is free of human interference (e.g. Atlas Bay and Long Islands in Namibia).

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ANNEX 1

Manual of methods for basic monitoring of Cape fur seals in the Benguela Current Ecosystem

Abstract

Procedures were presented for the three essential monitoring requirements that were identified for a "basic" monitoring programme in Benguela Current Ecosystem, based on seals. These included sampling and analysis of seal scats, estimation of pup numbers through aerial photographic censusing, and assessing mean pup mass and changes in mass. Besides drawing on information from the literature, knowledge and firsthand experience of various researchers in the field was appropriated and incorporated. Wherever possible, a theoretical background was provided with regard to sampling design and the analysis and interpretation of data. The need for carefully designed studies that have the various scales of spatial and temporal variability in mind, standardization of techniques and sampling dates to facilitate comparisons, and suitable sample sizes, was emphasised. Where relevant, requirements for further research to strengthen monitoring protocols, was highlighted. Four such areas include: (1) Investigating effects of sample sizes on the reliability of dietary estimates from scat collections; (2) further investigation of the loss rates of diagnostic prey structures during digestion, to allow for adequate compensation in prey abundance estimates from scats; (c) Calibrating for the effects of technological advances in equipment and techniques on the consistency of time series information (e.g. the conversion from black and white monochrome film photography to digital colour photography for aerial photographic censuses); (d) Investigating inter-annual and geographical differences in the timing of breeding and their potential effects on aerial census results.

Keywords: *Arctocephalus pusillus pusillus*, monitoring, diet, scats, population, abundance, census, pup, growth, cross sectional sampling, birth, mass

Contents

1. Introduction

In Chapter 8, proposals for a Cape fur seal *Arctocephalus pusillus pusillus* monitoring programme in the Benguela Current Ecosystem were presented. These were in line with the management objectives for the region (BCLME Top Predators Project Steering Committee 2007), and different potential scales of monitoring intensity (dependent on levels of financial support and regional co-operation) were considered when drafting them. In the three sections that follow, techniques are presented for the three essential monitoring requirements proposed for a “basic” monitoring programme in Chapter 8, namely faecal (scat) sampling and analysis, estimation of pup numbers through aerial photographic censusing, and comparisons of pup mass using the cross sectional sampling method. Also included is a procedure related to the latter, namely assessment of mean birth mass.

The manual provides users with practical information for sampling that has been drawn from reports, scientific papers and theses, and also attempts to consolidate the knowledge and firsthand experience of various researchers in this field (myself included). Where feasible, a theoretical backdrop for sampling design and the analysis and interpretation of data is provided. Emphasis is placed on the need for carefully designed studies that have the various scales of spatial and temporal variability in mind, standardization of techniques and sampling dates to facilitate comparisons, and the need for suitable sample sizes. Requirements for further research needed to consolidate, calibrate or improve upon procedures, are highlighted.

2. Estimating Cape fur seal pup numbers

2.1 Background

The pupping season of the Cape fur seal occurs during November–December each year, with most births taking place by mid-December (David 1987b). Pups are confined to the colonies and adjacent tide pools for a few weeks after birth (Shaughnessy 1987). Thereafter they venture into the sea adjacent to their colony, but they remain based at their natal colony until they are weaned at about 8–11 months after birth (David and Rand 1986, David 1987b). Assessments of the size and trend of the Cape fur seal population, or parts thereof, have been based on pup numbers, for various reasons:

- Pups are the only demographic category that is all confined to land, at least during their first few weeks of life;
- Their small size and the black pelage of their first ten weeks of life permit them to be easily distinguished from other age classes;
- Their small size permits them to be physically restrained for tagging and recapturing operations;
- Pup numbers can be used to infer adult population size (Shaughnessy 1987), subject to certain assumptions (Wickens and Shelton 1992), or provide input for population growth models (e.g. Butterworth *et al.* 1995).

Two techniques have been used to determine pup numbers, namely tag-recapture and counting. As direct counting of pups, from land or from the air, is not practicable due to the density of colonies, aerial photographs of the colonies are taken and the pups are counted on the photographs. Photographs provide a permanent, quantifiable record of the numbers and distribution of pups in the colony and, if more than one observer is used to count each photograph, a measure of inter-observer variability (Erickson *et al.* 1993). Given the intensity of effort required for tag-recapture populations (Shaughnessy 1993), the large size and widespread distribution of the population (Chapter 6), and the inaccessibility of many island breeding locations, the aerial census method is judged to be the most practical and cost-effective technique of censusing the population (Wickens *et al.* 1991), and is the approach described in this section. Aerial censusing is also the least intrusive method of censusing seal populations, as the disturbance effects associated with tag-recapture or ground counting are avoided (Erickson *et al.* 1993).

Although methods and methodology for determining pup numbers from aerial censuses have previously been comprehensively described in investigational reports by Shaughnessy (1987) and Cressie and Shaughnessy (1987), there have been several modifications to the technique since these reports. These modifications, which have come about due to the development of new technology, the large size obtained by some of the mainland colonies, or shortages of personnel and time for processing photographs and enumerating animals on them, are expanded upon in the sections that follow. Bias associated with the interpretation of aerial census results is discussed in Section 2.6.

2.1 Timing of censuses

- The timing of aerial censuses has been standardised to take place towards the end of the pupping season, specifically between about 16 and 24 December. This period presents a window of opportunity to estimate pup production when maximum numbers of pups (that are too young to venture into the sea) are expected to be present on the colony (Shaughnessy and Best 1975);
- Several colonies generally have to be covered on each census day. The hours per day dedicated to censusing is usually a trade-off between minimising the time taken for the entire census (to minimise expenses) and avoiding photographing at times when shadows are long – shadows may obscure pups, especially where there is uneven or boulder-strewn terrain (e.g. the colony at Jacob's Reef). A further consideration is that seals of all age classes tend to migrate closer to the water's edge in hot, windless weather, particularly on sandy beach colonies (e.g. the colony at Cape Cross). This causes clustering of large nursery groups of pups, which makes counting difficult. Because of time constraints, it may not be possible to restrict censusing to the morning, when temperatures are cooler. However, the effect can be minimised by aiming to census larger colonies in the morning, before temperatures reach their maximum;
- A comprehensive census of the population (South African and Namibian colonies) normally takes four–five days if the weather is favourable;
- Misty weather is the most unfavourable weather for the censuses, and photography frequently has to be delayed until mist lifts.

2.2 Aircraft

2.2.1 Fixed wing aircraft

Generally, pictures have been taken from a fixed wing aircraft. The aircraft should meet the following requirements:

- Twin engines, for safety;
- Ideally, a removable floor compartment with enough visibility to view the colony ahead of the flight-path, from which to photograph. However, this is not an option among South African commercial aircraft and the next best option is a removable luggage door in the rear;
- High wings and retractable wheels, so that the view of the colony is not impeded;
- Ability to fly slowly ($\leq$ 120 knots) into the wind;
- A wind baffle to protect the photographer from turbulence.

Most censuses have been conducted using a Partenavia aircraft, which fulfils these requirements.

2.2.2 Helicopter

Because of the difficulty of photographing the large Kleinsee colony (c. 3 km long) from a fixed wing aircraft in the strong cross-winds that frequently occur there, a helicopter (Jet Ranger) with extended fuel intake, has been used for this and other colonies along the west coast of South Africa in recent years. A helicopter has a number of advantages over fixed wing aircraft:

- Because it is difficult to correct the course of a fixed-wing aircraft while maintaining height during strong cross winds, transects along flight paths frequently have to be re-flown, wasting time and causing confusion with regard to which areas have been covered, resulting in duplication of photographs. A helicopter is less affected by cross winds because the pilot can simply hover and move sideways to prevent it straying from the flight path. Also, a helicopter can make shorter circuits and maintain altitude more readily than fixed-wing aircraft and, because of its lower speed and the fact that the recorder (see Section 2.4) has virtually all round visibility from his/her position in the cockpit, it is easier to keep track from a helicopter of which areas have been completed;

- Because a helicopter can fly at lower speed and follow a more accurate path than a fixed-wing aircraft and is less susceptible to thermal currents and wind buffeting that cause camera movement, it allows for more vertical, better quality pictures;
- Helicopters can land in virtually any terrain while waiting for mist to lift or rain to pass, whereas a fixed wing would need to return to a landing strip to avoid running out of fuel;
- With better quality pictures, less duplication and less likelihood of missing areas, the processing and fitting together of pictures (see Section 2.5) taken from a helicopter is less complicated and time-consuming than when a fixed wing aircraft is used.

On the other hand, censusing with a helicopter is more expensive (nearly double the cost per hour) than with a fixed wing aircraft which is able to fly longer distances without refuelling. Also, recent technological advancements in camera technology have mitigated for the poor quality of photographs taken from fixed wing aircraft at large colonies in turbulent conditions (see Section 2.3).

2.3 Photographic equipment

2.3.1 Black and white monochrome film photography

Black and white photographs have generally been taken using large format cameras. According to Erickson *et al.* (1993), large format aerial photographs facilitate easy counting of seals and minimise the problems of marking out areas that have been photographed more than once. To avoid having to change film regularly, the camera was fitted with a back capable of holding a large roll of film. Initially, a Hasselblad ELM fitted with an 80 mm lens and a large back with about 120 frames of film, was used. This camera was limited by its shutter speed (1/500 sec at best) which, combined with the speed and the height of the aircraft (c. 350 ft), frequently caused images to be blurred on account buffeting. The Hasselblad was replaced by a Pentax 645 fitted with a 75mm lens. The Pentax could take a similar number of frames and had the advantage of a more rapid shutter speed (up to 1/1000 sec), allowing for better quality photographs. Cameras were fitted with a motor drive so that photographs could be taken continuously in rapid succession, and set with speed as the priority.

Initially, 70 mm Ilford FP3 black and white film was used. However, this was replaced by Agfa Aviphot 70mm Pan 200 ISO. Pictures may be adjusted artificially by down-grading the ISO setting to 160 and consequently increasing the aperture. All black and white pictures were initially printed on grade 1 Ilford glossy paper, for sufficient contrast. However, this was difficult to obtain after the introduction of multigrade paper, which renders prints with poorer contrast. Therefore, Kenthene Grade 0, and more recently, Grade 1, glossy paper, were used, though the contrast of the prints did not match that given by grade 1 Ilford glossy paper. A3 size photographic paper was used for all black and white prints.

2.3.2 Digital colour photography

Digital cameras capture images in digital form and store them onto memory cards, from where they can be transferred to a computer. Use of digital cameras for censusing has a number of advantages over the large format film cameras. These include:

- "Instant feedback" (on the LCD screen) allows the photographer to judge the quality of pictures he/she is taking, or whether any areas have been missed during transects, while in the air. Thus, the photographer is in a position to determine whether to redo transects before flying to the next colony. With film cameras, the quality of photographs can only be judged after printing;
- The memory cards on which digital images are stored can be replaced as soon as storage capacity is reached. Changing of memory cards is quicker and easier than changing black and white film between photographing. A laptop computer with sufficient hard disk space to download the files from the memory cards can be taken on the census;
- The most up to date digital cameras can shoot several hundred images in sequence, as opposed to a maximum of about 120 when using black and white film;
- Potential mechanical failure such as jammed film is eliminated;
- With sophisticated digital cameras, ISO ratings can be extended, meaning that higher speed or narrower f-stop settings can be achieved than with a film camera. Therefore, better quality photographs can be taken and under poorer light conditions. This helps eliminate problems sometimes encountered when counting on black and white photographs, such as confusing pups with shadows or with 2nd year individuals of the same size;
- Digital images can be viewed and edited using photo software such as ADOBE Photoshop. Image quality (particularly contrast and brightness) can be enhanced to aid in distinguishing pups and incorrect exposure or shadow can be almost

eliminated. Magnification beyond that which can be achieved for the A3 film prints, can be achieved;

- The digital format is amenable both to archiving in a computer environment and in the form of a hardcopy product similar to regular prints (although colour prints of digital images are likely to fade eventually);
- It is possible to count pups digitally using Photoshop, or on hard copy prints. At least in the case of smaller colonies photographed using a digital camera, it is possible to tile the overlapping images together into a composite using Photoshop, and mark and count the pups digitally;
- Although a digital camera and accessories are expensive and therefore require a substantial initial investment, consumable expenses such as film and photographic paper (which has to be ordered from overseas suppliers) are eliminated, while the cost of photographic chemicals are largely offset by the cost of colour laser cartridges;
- The development process for the long reels of black and white (c. 120 frames) film used by the large format camera is time consuming and may be subject to various delays as specialised equipment retained by the South African Air Force is relied upon. Via Photoshop, digital images can simply be printed on standard Rotatrim A3 paper, using a high quality colour wax printer;
- The digital format revolution has meant that standard film equipment and products are fast becoming difficult to obtain.

The first digital camera that was tested by South Africa’s Department of Environmental Affairs (DEA) during censuses was a Nikon D1. This was used experimentally at a few small colonies during the 2002 (December 2002) census. A Nikon D1X was later tried in the 2004 census and a Nikon D2H in the 2005 census. More recently (2006 census), a Canon Eos 5D was tested and the entire seal census was photographed using this format. Initial problems with digital photography included:

- Cameras initially did not have the capacity to store successive photographs fast enough, causing interruption of sequences and loss of coverage;
- Area coverage (per frame) did not match that of the large format cameras.

For these reasons, digital photography was at first suited only to small island colonies. Such problems were largely resolved with the acquisition of the Canon Eos 5D, which has a full frame sensor that allows for area coverage similar to that of the large format cameras. Capacious memory cards (≥ 8 gigabytes) allow for taking of several hundred shots in rapid sequence. However, digital photography is a recent innovation that is developing rapidly, therefore further experimentation is likely during forthcoming censuses.

2.4 Photographic procedures

- For large colonies it is necessary to take high altitude pictures (c. 1000 ft) of the colony to assist with fitting of lower altitude prints to map the colony. These are generally taken before the lower altitude pictures;
- Each colony has to be covered with a series of vertical or near-vertical overlapping photographs from the lower altitude (c. 350–400 ft). There must be sufficient overlap to recognise features around the perimeter of the frame (10–20 %). To achieve this, it is necessary to fly parallel transects over each colony;
- From the fixed wing aircraft, photographs are taken out of the luggage compartment door in the rear (if there is no removable floor compartment), which must be removed before take-off. If a helicopter is used, photographs must be taken out of the rear door immediately behind the pilot, which also will need to be removed prior to take-off. Because the photographs are taken between the landing strut and the body, the step-up which runs across the landing strut must be removed;
- The photographer must always be accompanied by an assistant whose task is mainly to keep records. The recorder must note the start and end times of each transect and the numbers of frames used, and describe (or map) the sub-section of the colony that was covered. If a film camera was used, details such as aperture, shutter speed and ISO must all be recorded (this is recorded automatically in digital photographs). After completing a colony, the recorder must note the following details on an A4 page, which is photographed as a film break and record for the colony: (a) colony name, (b) date, (c) frames used, (d) film/card number. After each colony the recorder should also note the types of equipment used (e.g. camera type), the altitude flown at, and any environmental conditions that could have affected photography, including wind direction and speed, cloud base and cover, and visibility;
- The photographer must have communication with the pilot and the recorder. Headphones should be taped to the photographers head to prevent them slipping. In

the fixed wing aircraft, the recorder sits behind the pilot, in a helicopter, he/she sits next to the pilot, where there is complete coverage of the colony;

- The photographer must have a safety rope attached at all times, adjusted to the correct length;
- In the fixed wing aircraft, the photographer leans forward against the rope and takes photographs out of the rear door while on his/her knees. In a helicopter (assuming it is a Jet ranger) the photographer lies across the entire back seat with his/her feet up against the far window, and leans over the seat to take photographs between the strut and the aircraft body;
- The photographer should be warmly dressed and in the fixed wing aircraft, is advised to wear protection (e.g. skateboard pads) on his/her knees;
- Irrespective of which type of aircraft is used, transects are started on one side of the colony and continued straight across. Once a flight path is complete, the aircraft is turned and the next, parallel flight path is flown from the same direction. The runs should be flown into the wind to reduce speed, if possible (and never with the wind from behind). In the case of mainland colonies, the shape and orientation of the colony will influence the direction of approaches but at offshore islands, the wind, rather than the shape and orientation of the island, generally dictates the approach direction;
- In the case of extensive colonies (e.g. large mainland colonies), it is advisable to divide the colony area into sections (demarcated by features such as points or bays). All the parallel transects of one section must be completed before moving to the next. This will help to avoid missing areas in the colony. For smaller colonies, each transect can easily be conducted over the entire length or width of the colony;
- In extensive mainland colonies, runs are normally commenced on the seaward side of the colony, although this may depend on the wind direction and strength. This is because pup numbers are greatest along the sea shore and it is desirable to cover the denser areas first in case the census is interrupted;
- It is important to maintain a straight flight path during transects. This may mean that for the inland transects of mainland colonies, seals may be absent or sparsely distributed in several pictures;
- After each transect, a frame should be taken of an object outside of the colony, such the sea or sky, to mark the end of transects.

2.5 Pup counting and estimating procedures

- After printing, pictures must be laid out in frame sequence to create a photographic mosaic of the colony. The boundaries with neighbouring, overlapping photographs need to be delineated on each photograph and duplicate pictures must be eliminated. High altitude pictures assist with the mapping process, especially where isolated inland groups of seals occur in large colonies;
- Pups (or older age classes if these are of interest) in each photograph must be counted by two separate counters. The pups are scored with a hand tally counter. Each visible pup on the prints can be marked with a red omnichrome pencil (these marks can be erased with 70 % ethanol). Alternatively, marks can be made on transparency paper fastened firmly over the photographs;
- Accuracy and precision of counts are improved by marking borders around localised areas of pups (i.e. the borders are drawn through open areas without pups) and counting within the borders (i.e. within "counting areas");
- The difference between the two counts for a counting area is expressed as a percentage of the larger count. If the difference is greater than 20 %, counting is repeated by a third counter, or as many extra counters as necessary until there are two counts within 20 % of each other. This avoids the inclusion of unrealistic counts resulting from counter error. The arithmetic mean of each counting area (a) is then calculated from these two counts (N_1 and N_2)

$$\_Y_j = \frac{{}_{1,a} + {}_{2,a}}{\quad} \qquad (1)$$

Any extra counts are discarded. The total count for a colony is determined by summing the means of all the counting areas. A measure of the error (Y) in the total count of a colony can be estimated from the following set of formulae:

$$V = \frac{\sum_{a=1}^{A} N_{1,a} + \sum_{a=1}^{A} N_{2,a}}{\quad} \qquad (2)$$

$$W = \frac{\left(\frac{N_{1,a} * V}{\sum_{a=1}^{A} N_{1,a}}\right) + \left(\frac{N_{2,a} * V}{\sum_{a=1}^{A} N_{2,a}}\right)}{\quad} \qquad (3)$$

$$X = \left(\frac{N_{1,a} * V}{\sum_{a=1}^{A} N_{1,a}}\right) - \left(\frac{N_{2,a} * V}{\sum_{a=1}^{A} N_{2,a}}\right) \qquad (4)$$

$$Y = \sum abs\left(\frac{}{W}\right) * 100 \qquad (5)$$

where “abs” is the absolute value. Y can be interpreted as the “mean weighted absolute relative difference” between the two sets of counts per counting area. For example, a Y-value of 5.5 indicates that the two counts of each counting area differed by 5.5 %, on average. Thus, Y provides a measure of dispersion of counts that can be used to infer the “quality” of the total estimate, whereby the lower the value of Y, the better the quality of the estimate.

2.6 Issues of interpretation

Aerial censuses are known to underestimate true numbers (Caughley 1977). For example, in the case of Cape fur seal pups:

- A proportion of pups die before the census and a small proportion may be born after the census;
- Pups may be hidden in crevices or shadows, or may form tightly-bunched pods that are difficult to count. Levels of concealment of pups are influenced by factors such as the time of day, weather conditions and the colony’s terrain.

Shaughnessy (1987) found the magnitude of such bias to be independent of the pup population size of colonies, and concluded that, despite being underestimates, counts from aerial photographs are still useful indicators of relative abundance. However, improvements in the quality of photographs due to changes in photographic equipment (colour images from digital cameras) and aircraft (use of a helicopter), which should result in greater accuracy of counts and less error, could potentially inflate estimates of the rates of change in numbers over time. Therefore, there is a need to calibrate the effects of technical changes, perhaps via duplicate censuses conducted using the alternative aircraft types or modes of photography.

A further potential source of error that can potentially affect comparisons of pup counts over time and space, concerns the timing of the census itself. The timing of pupping, which in most studies is represented by the median pupping date, could conceivably vary between years on account of environmental variables (Boyd 1991), and may vary geographically. With regard to the latter, the large latitudinal range of the Cape fur seal, especially since the recent northward extension of the breeding population (Chapter 6), may entail that there are significant differences in the median pupping dates across the range of the population, considering that the timing of breeding is affected by the timing of implantation which is in turn controlled by photoperiod (Boyd 1991, Temte and Temte 1993). An implication of inter-annual and latitudinal variability in the timing of pupping (and their possible interaction) for the aerial photographic census is that each census will include colonies in different stages of the breeding pattern, in terms of the proportion of pups that have been born and levels of neo-natal mortality. Therefore there is a need to investigate inter-annual and geographical differences in the timing of breeding and their potential effects on aerial census results.

3. Mass at birth and mass changes of Cape fur seal pups

3.1 Background and objectives

The pupping season of the Cape fur seal occurs during November–January each year, with females normally giving birth to a single pup (David 1987b). Between giving birth and weaning their pup (approximately 8 to 11 months after birth), adult female fur seals alternate foraging trips of up to about a week at sea with suckling periods of about two days in duration (David and Rand 1986, Gamel *et al*. 2005). Between weaning and the following pupping season, females return to sea for a long and intensive foraging period, before hauling out to give birth again (Rand 1955).

Annual changes in the average mass of pups at birth is considered to be a good indicator of foetal growth in the last few months of gestation, and therefore a possible indicator of food availability in the area where females forage before parturition (Boltnev *et al.* 1998, Georges and Guinet 2001, Lunn and Boyd 1993, Ochoa-Acuna *et al.*1998, Reid 2002). During the lactation period, mass gains by pups depend on provisioning by the mothers, therefore the growth rates of pups reflect the rate of energy transfer from mothers to pups, and provide a good indication of prey availability (Reid 2002, Beauplet *et al.* 2004). In addition, because fur seal mothers are central place foragers during the lactation period, the growth rates of pups should reflect conditions for which the spatial and temporal boundaries can be readily determined or estimated (Reid 2002). Boyd and Murray (2001) found pup growth rates of Antarctic fur seals *A. gazella* to be a more reliable indicator of ecosystem variability than other variables that were monitored over a 22 year period, including population size, breeding performance, foraging behaviour and diet.

This section describes methods for determining mass at birth and indices of pup growth rates of Cape fur seals, for comparison between years (or between locations).

3.2 Birth Mass

By weighing a suitable sample of pups at or soon after birth, the mean birth mass can be obtained, for comparison between years or locations. Other measurements besides birth mass can be obtained, e.g. standard length or axillary girth. However, it must be noted that it is more difficult to take consistent length or girth measurements of live animals from year to year, than mass, because resistance by animals (unless anaesthetised or dead) makes the process of measuring awkward. Also, there is greater potential for discrepancies between how different workers take length or girth measurements, than mass (Boltnev *et al.* 1998).

Considering the above and the likelihood that foetal growth in mass is more closely linked to environmental conditions than length, which may be more dependent on genetic regulation (Boltnev *et al.* 1998), birth mass is considered to be the more useful variable in terms of providing an index for comparison. It is also possible, by scaling body mass to body length, to obtain a body condition index (BCI) that may be a useful indicator of the health of pups at birth, as long as there is consistency in the measuring of length.

3.2.1 Equipment and personnel

- Because it is necessary to work in a breeding colony to sample birth mass of pups, the procedure is dangerous and should not be attempted by a single worker. At least two skilled workers are required and three is preferable if it is also necessary to mark pups or take additional measurements such as standard length. More workers would probably be superfluous and may be counter–productive in that the work party may be overly conspicuousness, at the cost of efficiency;
- A scale allowing for mass to be measured to a resolution of 0.05 kg. If an electronic platform scale is used, it would have to be small enough to be easily portable through the colony, and large enough for a pup to be placed upon it in a suitably sized box, without over-balancing. However, a suspension scale is probably more appropriate for weighing pups at birth because it is lighter and less awkward to transport around the colony. The scale should be calibrated prior to sampling;
- If a suspension scale is used, a rope (c. 1.2 m of climbing rope) with a loop on one end and a hook attached to the other can be used to suspend the pup from the scale. The hook end is passed through the loop to create a noose and attached to the scale

once the noose has been placed around the pup's body. Alternatively, the entire pup may be placed in a nylon bag, which is then suspended from the scale;

- The suspension scale should have a rope loop attached to the top, so that the scale itself can be suspended while the pup is hung from the scale (holding onto the scale itself while weighing, instead of suspending it, will result in incorrect readings);
- The ropes (and the nylon bag, if used) should not be longer than necessary otherwise workers will have to stand upright in order to have sufficient clearance from the ground to weigh the pup. Standing upright can cause disturbance to the colony;
- A suitable piece of equipment to take length measurements (if required) is a meter long wooden plank or an aluminium plate with a 1 cm resolution scale (e.g. with a linen measuring tape stuck to the surface). A linen measuring tape is suitable for girth measurements;
- A noose (choker) pole for capturing pups (Gentry and Holt 1982) – the pole should not be too heavy and cumbersome and should not be made of steel or aluminium because this could cause damage to adult's teeth if they attempted to bite it. A softwood pole (e.g. pine) is ideal. The pole should be at least 2 m in length and 5 cm in diameter, preferably with a rounded circumference (if square, the corners can be bevelled to an octagonal shape for a more comfortable grip). A hole must be drilled through the pole about 2–3 cm from the tip and another about 15 cm further from the tip. A length of rope (hemp) of about 1 cm in diameter is then threaded through the holes to form a loop (noose) and is knotted at each hole to secure the noose. Once tied, the noose rope should measure about 1 m so that when hanging freely from the horizontally held pole, it extends about 45 cm. If the noose is so limp that it collapses in on itself when hanging freely, it can be strengthened by tightly wrapping some tape around the rope;
- It is advisable to take a second pole (similar to the first) to use for safety. The "safety pole" is used to distract seals or deter them from approaching the workers. Either pole is likely to get bitten from time to time (breakage may occur if the wood has knots);
- A pair of scissors or a scalpel/sharp knife (for cutting the umbilical cord if the placenta is still attached);
- A means of marking pups if there is a possibility that the same pup might be re-sampled accidentally. Options are to clip some guard hair with a pair of scissors, or to mark the pelage with paint or hydrogen peroxide solution. If it is necessary to identify individuals in future e.g. for a longitudinal growth or survival study, then a unique

mark will be required. Ways of marking pups, temporarily or permanently, are discussed in Appendix 1.

3.2.2 Sampling procedure

- When approaching a harem or a mother-pup pair, care should be taken to minimise disturbance by approaching slowly from a downwind direction, preferably in a crouched or creeping position. Avoid creating a silhouette, e.g. by approaching from over a rise;
- Newborn pups may be located by observing births, the presence of a fresh placenta or of a fresh (un-dried) umbilicus if the placenta is absent, or the presence of dark green foetal excrement (CCAMLR 1997, Boltnev *et al.*1998). The placenta may remain bright red and bloody for 24 hours, but may become detached and/or destroyed by predators within this time. However, the placenta can remain attached to the pup for up to week in a blackened, dry state therefore the mere presence of a placenta does not necessarily indicate a new birth (Gentry and Holt 1982);
- Directly following birth, the female will nuzzle her pup and exchange calls with it. Causing disturbance or separating the pup from the mother before or during this critical process may compromise pup survival, because if the mother-pup bond fails to form, the mother may reject her pup (Doidge and Croxall 1984). Workers should wait until after mother-pup recognition has occurred;
- The new born pups may be captured by hand or by using the noose pole, depending on circumstances, including the attitude of the mother (e.g. aggressive or placid), or whether the placenta is still attached to the pup or not;
- To use the noose, the pole is extended towards the pup and the noose placed over the pup's head and hooked beneath one fore-flipper. This placement of the noose encircles part of the rib cage and prevents closure of the trachea if the pup is lifted off the ground (as could occur if the noose was only around the neck). The pole is then rotated along its longitudinal axis so that the noose tightens, and the pup is gently raised slightly off the ground and drawn towards the workers. Alternatively, the noose may be placed from the rear, and tightened around one hind-flipper. As there is more chance off the noose slipping off a hind flipper than the torso, the pup should be dragged gently along the ground in this case;
- The workers should remain in a crouched position all the time, and avoid making any rapid movements, while using the noose pole. They should also avoid waving the

noose pole about in the air when trying to place the noose over the pup – rather, the pole should be extended towards the pup at ground level, then the tip raised to just over the pup's head, before the noose is placed over the pup's head or flipper;

- If the mother is aware of what is taking place and becomes alarmed, the second worker can slowly extend the safety pole towards her until the end is in front of her nose. In most cases, the mother will pause to sniff the pole;
- This distraction may buy enough time for the first worker to remove the pup from the noose, retreat slightly and turn so that the pup is out of vision of the mother, then sex, weigh and mark the pup. Slightly more time is required if it is necessary to take other measurements (e.g. length), or apply one or more unique markers to the pup;
- If the mother continues to advance (e.g. it may be attracted by the cries of the pup), the second worker should lower the safety pole to the level of her chest. Most females will pause if they walk into the tip of the pole, and sniff at it again. By then lowering the pole still further and gently tickling her fore-flippers with the end of the pole, she may be induced to retreat a little (NB: only in dire emergencies should the safety pole be used with any force);
- If the mother is aggressive or frantic and persistently tries to reach her pup, it may be necessary to return her pup to her before sampling can be completed to prevent undue stress, and in the interests of human safety;
- If the mother manages to grab hold of her pup while it is held in the noose, the noose must be loosened by quickly turning the pole to allow the mother to remove the pup from the noose without injuring it. If the pup remains hooked in the noose while held by the mother after the noose has been untwisted, it may be necessary to release the pole to prevent a tug of war situation, and retrieve the pole once the mother has put the pup down (this is another reason why a light pole is preferable);
- If the placenta is still fresh and attached to the pup, it may not always be advisable to use the noose pole, depending on the terrain or the state of awareness of the mother. If the dangling placenta is grasped by the mother or snags upon something (e.g. a rock) while the pup is being withdrawn, injury could result to the pup;
- If the mother is sleeping, or is awake but not at all alarmed by the approach of the workers, it may be possible to withdraw the pup by hand. If the placenta is still attached, care must be taken to prevent it snagging on any object. In this case the pup can be held by the hind flippers with one hand, while the other hand supports the pup under its chest and at the same time holding the placenta;

- The placenta (if attached) has to be removed before the pup can be weighed. Simply cutting the umbilical cord will cause bleeding if it is still fresh. A simple “overhand” knot (the first step of a shoelace knot) can be tied in the umbilical cord and the chord then cut at the placental end of the knot (alternatively a piece of string can be knotted around the chord to constrict it);
- Because there is always a risk of being interrupted by the mother or by a male during the procedure, it is advisable to sex the pups (by inspecting the vent) before they are weighed. Knowing the sex without the weight has some value (i.e. sex ratio at birth) but because mean birth mass between the sexes is significantly different (NATMIRC unpubl. data), knowing the weight without the sex is of little use;
- The scale should be zeroed before weighing each pup, with the bag or rope attached to it;
- If a rope is used, the easiest way to place it around the pup is for the worker to wear the noose around the wrist of one hand. Take the pup by the hind-flippers with the same hand, and use the other hand to reposition the noose to the pup’s chest, with one fore-flipper under the noose and the other one over (make sure at least one fore-flipper is over the noose or the pup shall be hung around the neck). Gently pull the noose tight then suspend the pup head upwards from the suspension scale;
- The suspension scale itself can be suspended by one (strong) worker holding the rope loop at the top of the scale, or else one of the poles may be passed through the loop and held by a worker at each side;
- If standard length is to be measured, then after weighing hold the pup belly down on the measuring board with its nose against the wooden block. Straighten the body by pulling gently on the hind flippers, and take the measurement to the tip of the tail;
- Mark the pup, if necessary (see Appendix 1);
- After sampling is completed, care must be taken to return the new born pup to its mother’s side. This should be done slowly, so that the mother has the opportunity to inspect the pup – pups thrust at their mother’s side may get bitten (CCAMLR 1997). Newborn pups not returned to their mother may wander unprotected and approach aggressive females. Pups may be returned by hand or by using the noose pole, depending on circumstances;
- The workers always need to be wary of the territorial males, which naturally pose the greatest danger to the safety of the workers. An approaching male will nearly always come to a halt if his chest comes into contact with the tip of the safety pole, and he

will pause to sniff the pole. By then lowering the pole and gently teasing his fore-flippers, he can be induced to retreat. Some males may be satisfied after biting the pole once. Males may also be distracted by other means, e.g. rousing a female at the opposite side of the harem by targeting her with a few small pebbles might attract the male towards her. However, a small percentage of individuals will not be deterred, in which case it may be necessary to move out of danger. Only in dire emergencies should the safety pole be used with any force.

3.2.3 Considerations for sampling

3.2.3.1 The timing of sampling

Generally in the pupping season, few births occur before 15 November, and most births have taken place by mid-December (Shaughnessy and Best 1975, David 1987b). The size of new-born pups may change as the pupping season progresses, corresponding to changes in the size and age of females giving birth, as previously has been demonstrated for Antarctic fur seals (Boyd and McCann 1989). For Cape fur seals, it has been noted that the sex ratio at birth is skewed towards female pups near the beginning of the season and male pups near the end of the season, and that male pups are, on average, significantly heavier at birth than females (NATMIRC unpubl. data). It is therefore desirable for sampling to be distributed over the course of the pupping season, to avoid any influence of the above on “spot” samples (samples obtained during a brief window period). Furthermore, the timing of pupping may vary between years (and locations) with consequence for spot samples taken on a fixed date. For example, following years characterised by poor feeding conditions, parturition was delayed among Antarctic fur seals at South Georgia, probably due to a delay in the timing of implantation (Boyd 1996).

3.2.3.2 Sample sizes

Spot samples of pups weighed at birth should contain no less than 50 pups of either sex to be able to determine dependable confidence intervals about the mean. Naturally, higher sample sizes are desirable if they are obtainable. If sampling is conducted throughout the pupping season, it should be possible to attain well over a hundred pups of each sex. If pups weighed at birth are required for a longitudinal growth study, an initial sample of 75–200 pups (sexes combined) is desirable CCAMLR (1997), depending on the ease of recapture (see Section 3.3.1). If the pups weighed at birth are to be monitored subsequently to determine survival rates, an initial sample size of no fewer than 500 pups should be aimed at.

3.2.3.3 Study areas

The size of pups at birth may also be related to where they were born in the colony. Larger, more experienced females that give birth to larger pups would be expected to inhabit primary breeding space, limiting first time breeders (which tend to give birth to smaller pups) to the periphery of the colony. The distribution of sampling effort should take such variability into consideration. Therefore, if pups are to be sampled within a demarcated study area, the area should consist of a cross section of the colony from the coast inland.

Sampling birth mass of all or most of the pups born in a discrete study area is an intensive and potentially disruptive process. Even if workers operate cautiously, the disturbance they cause is likely to result in a reduction of births in the same area in the following year (see Chapter 4), by causing some females to re-locate to other areas for their next birth. Consequently, if the same study area is sampled in consecutive years, the females giving birth in the area may be skewed towards first time breeders (that have not previously encountered investigator disturbance), in which case the samples will not be representative of the population. Therefore, if it is necessary to sample within a discrete study area, it is advisable to rotate the location of study areas between years.

3.2.3.4 Worker safety and minimising of disturbance

The pupping season is the most dangerous time of year to work in a fur seal colony because of the density of animals and the high levels of aggression, especially among males. The following should be kept in mind:

- Sampling should not be attempted by a single worker;
- Gentry and Holt (1982) caution that when fur seals bite, they usually make a single tearing slash at the surface of their target. Workers may therefore be spared injury by wearing loose fitting clothing. However, clothing that flaps noisily in windy conditions may cause disturbance and compromise the efficiency of sampling;
- Workers should use a safety pole to deter or distract seals (see Section 3.2.2). The pole should never be used with force (except perhaps in dire emergencies). If a male (or a female) is not deterred by the pole and attempts to attack the workers, it is

usually not appropriate to bolt and run, but rather to withdraw cautiously – overreaction to an attack by one worker can jeopardise the safety of co-workers (Gentry and Holt 1982). In cases where a male (or female) cannot be deterred from attacking workers, it may be best to simply move away from its location and work elsewhere, in the interests of safety and minimising disturbance;

- Workers should attempt to keep a low profile and move slowly at all times, both when approaching animals and while working with them. Voices should be kept down, equipment (e.g. the scale) should be prevented from banging and rattling on rocks, and elongated equipment (e.g. poles) should not be held upright;
- Workers should try to use the wind to their advantage. Generally, this will entail working into the direction the wind is coming from, as Cape fur seals become skittish when they smell humans. However, in some cases, it may be to the worker's advantage to be detected sooner, rather than later, e.g. to avoid a stampede while working in amongst animals, as a result of animals becoming aware of them suddenly for the first time. In this situation it may be better to approach from the windward direction;
- Generally, one should avoid making eye contact with either males or females during the pupping and mating season. It is better for workers to keep their faces slightly averted from the seal's gaze, and only glance occasionally at them, or observe them out of the corner of the eye;
- Most importantly, according to Gentry and Holt (1982), workers should be familiar with the behaviour of the study animal – knowledge of how animals act and are likely to react reduces one's fear and fosters the calm judgment that working under these conditions requires.

3.2.4 Analysis

3.2.4.1 Birth mass

The mean and the variance of the mass are comparable between years or locations. Multi-way analysis of variance (ANOVA) can be employed to compare birth mass statistically between years at the same location (or between different locations in the same year or between multiple years and locations), in this case with sex of the pup and year as the independent variables and mass the dependent variable. Alternatively, a convenient multi-year index of annual mean birth mass at a location that allows the deviation from the long term mean birth mass to be determined for any given year, can be developed as

$$d_i = m_i - \left(\frac{\sum_{i=1}^{n} m_i}{n} \right) \tag{1}$$

where d is the deviate of the mean birth mass m in year i, from the long-term mean birth mass of n years (based on Reid 2002). Separate indices should be developed for male and female pups.

3.2.4.2 Body condition index at birth

In the past, pup mass (kg) / standard length (cm) has been used as a body condition index (BCI). However, according to Guinet *et al*. (1998) this ratio is not a good index of pup condition because it is not independent of length. A more appropriate BCI can be determined from the residual values of the relationship between mass of pups and their standard lengths (Guinet *et al.* 2005). This requires pooling the pup mass and length data from different years. To standardise, equivalent numbers of pups with length-mass measurements at birth should be included from each year. This entails that the number of measurements pooled from each year is determined by the year(s) with the lowest sample size. In this case, the measurements used from the years with larger sample sizes must be randomly selected from the measurements available in each of those years.

With the measurements from all the years pooled, the BCI of each individual pup is calculated as the difference between its observed mass and the expected mass for a pup of its length according to the relationship in the previous paragraph (Guinet *et al.* 2005). Therefore the BCI’s of pups born in years with favourable conditions will be expected to be mostly positive, and the converse would be expected in unfavourable years. Annual BCI’s can be determined by summing the pup BCI’s of each year, but separate BCI’s should be determined for male and female pups.

3.3 Cross sectional sampling

Measuring the mean change in pup mass during the lactation period, or an index thereof, may provide as an indication of prey availability to the mothers. In this regard, pup mass is a more useful variable to measure than e.g. length, which is less likely to be dependent on feeding conditions. Changes in offspring mass with time can be determined either via longitudinal (serial) sampling, whereby the same individuals are weighed repeatedly over a period of time, or cross sectional sampling, whereby a random sample of different individuals in the population are weighed at pre-defined intervals. Each approach has advantages and disadvantages.

Longitudinal sampling is more precise and involves working with individually marked pups. It is however, more labour intensive and potentially more disruptive to colonies – regular disruption of colonies and handling of study animals can in fact retard the pups' growth and compromise results. Moreover, locating, capturing and weighing a sufficient number of pups to characterise changes in mass of the pup population can be so time consuming that it is often not practical as a routine operation (Reid 2002). Longitudinal sampling of mass changes in pups is therefore not recommended for basic monitoring (Chapter 8).

Cross sectional weighing offers a more straightforward approach than longitudinal sampling because random samples of pups are weighed at intervals and there is no requirement to recapture the same pups. However, this approach is prone to several biases, including that (a) the choice of individuals to sample may be affected by size or habitat choice of individuals, and (b) in periods of low food availability, the mortality of smaller pups can cause the mean mass of live pups to be biased upwards (Trites 1993, Reid 2002). These are discussed in the sections that follow.

3.3.1 The suitability of cross sectional sampling for estimating mass changes

Cross samples can be used for comparison of mean pup mass or change in mean pup mass between years (or locations). This can be done in the following ways:

- Comparison of the mean pup mass determined by cross sectional sampling on the same date in different years (or locations);
- Comparison between years of the mean rate of mass change of pups, determined by fitting a linear regression to cross samples conducted at intervals of time.

The second approach has been followed in several studies (e.g. Doidge *et al.* 1984, Bester and van Jaarsveld 1997, Kirkman *et al.* 2002). A problem with the approach is that a high mortality of starving pups can inflate the perceived rate of mass change and obfuscate any signal from the time series (Reid 2002). That is, a perceived increase in mass over time may be interpreted as growth whereas it is in fact an artefact of light pups being removed from the sample. Another problem with the second approach is its inherent assumption that growth patterns are similar between years (or locations). Reid (2002) found that the assumption of a linear growth pattern did hold true in every year, with regard to the Antarctic fur seal (which has a lactation period of 3–4 months), therefore it could not be assumed that the slopes of the regressions were good indicators of growth differences between years.

Considering the above, Reid (2002) considered inter-annual differences in growth rates derived from cross samples to be unreliable indicators of inter-annual differences in feeding conditions experienced by the Antarctic fur seal population. The same is likely to be applicable to Cape fur seals, which are weaned after 8–11 months. In most years, the growth curve of Cape fur seal pups is likely to be sigmoidally shaped rather than linear, similar to the subantarctic fur seal *A. tropicalis* which also has a lactation period of comparable duration (Guinet and Georges 2000). Considering the variable nature of the Benguela Current Ecosystem, the growth pattern of Cape fur seal pups may be characterised by considerable variability between years.

Reid (2002) concluded that comparisons of growth rates based on cross sectional sampling should not rely on underlying assumptions of growth pattern. Comparing mean pup mass at specific ages between years (or locations), without attempting to estimate rate of mass change over time (the first approach above), avoids the above complications. He therefore developed an index based on the deviation of mean pup mass at age from the long term mean for that age, to serve as an indicator of variability in feeding conditions between years. This approach relies on consistency in the timing of sampling between years (or locations), which can be problematic from a logistical perspective (discussed further under Section 3.3.2)

3.3.2 Considerations for sampling

3.3.2.1 Obtaining representative samples

In any sampling protocol involving the capture of highly mobile subjects, it is likely that samples will be biased in some or other way, such as with regard to size or habitat choice of individuals (Trites 1993). For example, attempting to chase down pups in the colony for weighing will tend to favour weaker pups or pups that are full from suckling. Opportunistically weighing only the most easily accessible pups (e.g. pups at rest along the perimeter of the colony) can also introduce bias because there may a degree of spatial segregation with regard to the size, age, sex or condition of pups within the colony. Therefore, to obtain a representative, random sample, it is recommended that groups of pups should be rounded up and the pups within each group weighed indiscriminately. If the terrain of a colony is heterogeneous, with significant numbers of pups occurring on different terrain types (e.g. rocky areas and sandy beaches), the distribution of sampling effort should ideally take this into account.

3.3.2.2 Sample sizes

If samples are to be compared for statistical differences (e.g. between years) or used to construct growth curves, then large samples are required as a rule (Trites 1993). This is because large variability in body mass between pups, attributable to such factors as whether the pup is currently fasting or has recently fed, is typical. Furthermore, considering that variability in body size increases with age, increasingly large sample sizes are required (in theory) with increasing age of pups (Trites 1993). From a practical perspective, however, it generally becomes increasingly difficult to obtain large samples as the pups grow older, due to the increasing size, strength and mobility of pups, and the fact that spend increasingly longer periods of time in the water. Effects of sampling large numbers of pups on the colony also need to be kept in mind, because considerable disturbance can be caused.

As a benchmark, it is recommended that sample size targets of not less than 50 male and 50 female pups be set for each cross sectional sampling occasion. Based on these minimum sample sizes it was possible to show relationships between mean mass of Antarctic fur seal pups at South Georgia and prey availability over several years of study (Reid 2002). However, it is recommended that larger sample sizes (as many as 100 of each sex) should be obtained if it is practicable and can be done without undue disturbance.

During sampling, the sex ratio of pups that are caught and handled is invariably biased in favour of males, implying that it generally takes longer to obtain the target of females (although this is not always the case). If the target number of males has been achieved, workers should avoid selecting pups for weighing that are judged from appearance to be females, because this can result in bias. Sampling should continue indiscriminately, preferably with all the extra male pups that are handled being weighed, until the female target is fulfilled. It is in fact beneficial to have larger sample sizes of males than females; males are heavier than females, on average, therefore larger sample sizes are required to detect statistically significant differences between samples of males (Trites 1993).

3.3.2.3 Consistency in sampling effort

It is important to follow the same procedure between sampling occasions so that any hidden biases are consistent between samples (Trites 1993). This includes the spatial distribution of sampling in the colony and procedures for rounding up and weighing pups. Ideally, sampling should be conducted on (or close to) the same date in different years (or between locations) (Trites 1993).

3.3.2.4 Timing of sampling

Cross samples should not be conducted before the pupping and mating season is finished, because the procedure is disruptive to the colony and may indirectly cause mortality of new born pups. In most monitoring studies (e.g. Kerley 1985, Bester and van Jaarsveld 1997, CCAMLR 1997), cross samples are not conducted until a month after the median pupping date.

Because cross sectional sampling entails measuring the mean mass at age of pups, the age of pups has to be determined. Generally, the number of days from the median (or mean) pupping date is used as an index of pup age. Unless the timing of pupping is accurately quantified for each year in the comparison, a common median date must be assumed for all years, with the assumption that there is little variation in the timing of pupping between years. Cape fur seal median pupping dates that have been estimated in previous studies include 3–10 December at Atlas Bay (de Villiers and Roux 1992), 7–8 December at Wolf Bay (de Villiers and Roux 1992), 4 December at van Reenen Bay (David 1987) and 1 December at Seal island in False Bay (Shaughnessy and Best 1975).

3.3.3 Sampling procedure

3.3.3.1 Rounding up of pups

How to approach the rounding up of pups will depend largely on the terrain of the colony. In flat terrain (e.g. sandy beaches), netting covered aluminium frames (at least 5, of 2m * 1m) joined to form a portable corral, are useful for containing pups. At least 6 workers are required to run with the joined frames if there are 5 of them, holding them at the two ends and at the joins. Ideally, there should also be two independent, individual herders. The workers holding the frames have to run in a straight line, upwind and parallel to the shore, to cut pups off from the sea. The pups will attempt to reach the sea, but by maintaining a straight line while running with the frames, the pups will be herded in the upwind direction. Larger, faster pups will tend to move to the front of the column, while the slower individuals accumulate at the back. One of the independent herders has to herd the trailing pups to prevent them stopping and being overtaken by the line of frames. The second independent herder generally runs on the seaward side of the frames, ready to lend assistance where required.

At a crucial stage, the leader bends the line of frames into an arc by turning inland, and stops, thereby cutting off a selected number of pups from heading further. At the same time, the independent herders cut off pups at the trailing edge of the line of frames, so that pups are guided into the corral along a corridor. Any larger animals (older than pups) have to be chased past the edges of the corral by the herders, or, if they are encircled, allowed to escape under the corral by raising some frames. The pups to be weighed are then entrapped and excess pups can be blocked off by closing the corral.

In colonies with irregular terrain, groups of pups may driven to a suitable area before being surrounded by a corral, or else they may be trapped against an embankment or herded towards a bottleneck in the terrain (e.g. an opening in a gulley) and contained there (e.g. by folding the line of frames to a suitable size to block escape).

3.3.3.2 Weighing of pups

The pups tend to climb on top of each other when surrounded, but weighing only the most accessible pups e.g. those on the outside or on top of a pile, can result in bias (Trites 1993). Therefore every effort must be made to weigh pups in a group indiscriminately. On some occasions, it may be necessary to hasten the processing of a group, e.g. to prevent over-heating. To facilitate the even distribution of weighing throughout an area, smaller, more numerous round-ups are preferable to securing a large group of pups at one time. The latter also increases the danger of over-heating or suffocation among pups.

The equipment required for weighing are basically the same as in Section 3.2.1. If an electronic platform scale is used, it must be large enough for a suitably sized box (e.g. plastic crate) to be balanced on top with a pup inside. Alternatively, a suspension scale on a tripod can be used. A tripod has the advantage of being less awkward to transport around a colony than a platform scale. A suitable tripod should be strong but light enough to be easily portable (e.g. aluminium), have flexible legs that can be folded together for transportation and adjusted to obtain balance on uneven terrain, and have sufficient height for the suspended pup to be clear from the ground. Alternatively, the scale may be suspended from a pole held between two workers, but a tripod is recommended because this frees up two workers from having to hold a pole continually during weighing. Pups can best be caught by hand, by clutching one hind flipper at its base. If a suspension scale is used, the rope is placed around the pup which is then suspended by the rope from the scale, as described in Section 3.2.2. The sex and the weight of each pup must be noted.

An electronic scale may be preferable when pups are older (e.g. between July and weaning) and capable of inflicting serious bites, because this method of weighing is safer and less strenuous than suspending the pups. At this age a small hoop-net with a PVC cone blindfold may be useful for catching pups (e.g. within the corral).

3.3.3.3 Personnel requirements

At least six workers are required for a cross sample weighing operation, but eight or more workers are desirable. In general, all personnel will engage in the rounding up of pups for weighing, bar one worker who transports the equipment (or two, if a heavy platform scale is used). While weighing is taking place, 3–4 workers (depending on the number of pups caught) will be engaged in observing the group of trapped pups to prevent any from escaping and to avert the risk of over-heating or suffocation among pups. The remainder will be engaged in handling and weighing the pups with one person recording information.

3.3.3.4 Worker safety and preventing pup mortality

Once they are contained, pups tend to clamber over one another in an effort to escape, often resulting in a pile-up. Pups at the bottom of the pile are at risk of over-heating or suffocating. To prevent any pups from being trapped at the bottom for too long, pups should be physically removed from the pile at frequent intervals and placed next to it. Workers need to watch out for any signs of distress among pups. Under no circumstances should groups of pup be contained on terrain with puddles of water because pups at the bottom of the pile will be at risk of drowning.

Ideally, the number of pups contained at a time should not exceed about 30. This will prevent unmanageable pile-ups and will allow for each group to be speedily processed, so that any stress that pups are placed under is not prolonged. Sometimes more pups may be trapped than intended. If necessary, the processing of a group of pups can be speeded up by weighing only every second or third pup taken from the group, and releasing the others without weighing them. However, on some occasions, it may be necessary to release pups en masse before they can be sampled, in order to prevent pups from over-heating. To avoid such situations, it is recommended that sampling is conducted in the early morning, before the air temperature rises. Days with “berg” wind conditions should be avoided.

Minor nips are almost inevitable when working with large numbers of pups. These can be minimised by wearing loose-fitting clothing and gloves. All bites should be treated with anti-sceptic. When pups are 9–10 months old or older, bites can be quite serious and may need to receive treatment.

3.3.3.5 Harvested pups

In the past, the mass of pup carcasses has frequently been cross-sampled following harvesting (usually from July or August onwards). However, such samples are biased, and should not be compared with live cross samples for the following reasons: (a) the sealers are supposed to bleed the pups directly after clubbing them (thus reducing the mass of carcasses) and (b) sealers tend to select for larger-sized pups, therefore the samples are not representative.

3.3.4 Analysis and interpretation

As long as the timing of sampling occasions is consistent between years, the same applies as for Section 3.2.4.1.

4. Monitoring the diet of Cape fur seals using scats

4.1 Background

Most published works on the diet of the Cape fur seal have been based on stomach content analysis. Stomach samples have been collected from animals that were harvested, drowned in fishing operations, stranded on beaches, or shot at sea during dedicated censuses (Rand 1959, Shaughnessy 1985, David 1987a, Lipinski and David 1990, Castley *et al.* 1991). The diet of seals stranded, harvested or drowned in nets provides inadequate indicators of diet composition, the reasons being that the diet of stranded seals is by nature biased towards individuals in poor health, seals killed in fishing operations are likely to have been scavenging, and only certain sex-age classes are targeted during harvesting (subadult and adult males, pups), which takes place in only a part of the population's range and at certain times of the year.

Advantages of sampling seals encountered at sea include that the foraging location of sampled animals is known (Harwood 1992). However, the technique is extremely expensive and time-consuming, and because it is lethal it is increasingly regarded as unacceptable on moral and aesthetic grounds (Pierce *et al.* 1991). It is also subject to practical problems regarding obtaining random samples (Butterworth and Harwood 1991) and adequate sample sizes (Harwood 1992). Further, interpreting the stomach contents of sampled animals can be difficult as different prey items may pass through the stomach at different rates, causing prey composition in the stomach to be a biased representation of prey consumption (Harwood 1992).

Other methods of investigating seal diet include the analysis of stomach contents obtained from stomach lavaging or from natural regurgitations, analysis of scat (faecal) material collected from rookeries or obtained via an enema method, and molecular analysis of tissue samples. Stomach lavaging is intrusive and subject to similar biases and limitations as the sampling of shot individuals (Harwood 1992). Natural regurgitations have been used to investigate the diet of some fur seal populations (Fea *et al.* 1999, Kirkman *et al.* 2000), but are seldom encountered in Cape fur seal rookeries (pers. obs.). Relatively new techniques such as analysis of fatty acids or stable isotopes, which rely upon samples of accessible tissues such as blood, muscle, blubber, milk or fur (Staniland and Pond 2005, Todd *et al*. 2010) may be useful for confirming temporal shifts or geographical differences in dietary intake of fur seals (Kurle 2002, Lea *et al.* 2002, Bradshaw *et al.* 2003, Hall-Aspland *et al*. 2005), but are extremely expensive for basic, region-wide monitoring.

In recent years, analysis of scat material collected at colonies has been the preferred method of investigating fur seal diet (Trites and Joy 2005). In southern Africa, this method has been employed for sampling the diet of Cape fur seals at mainland colonies in Namibia (see de Bruyn *et al.* 2005, Mecenero *et al.* 2006a) and at breeding and non-breeding colonies in the Eastern Cape province of South Africa (Stewardson 2001). As with stomach sampling, the method is subject to many limitations and biases (see Section 4.6.1), but nevertheless can provide important information on spatial and temporal trends in the relative consumption of the main prey species (Tollit and Thompson 1996), as well as quantitative information that may be useful for the management of fish stocks (e.g. Roux 2007). Compared with at-sea sampling of seals for dietary information, the technique is extremely cheap and practical.

The procedures described in this section are relevant to assessing diet composition of fur seal populations based on scat analysis and detecting changes in diet with time and location. Attention is given to alternative sampling techniques that are compatible with meeting these objectives (e.g. pooled sampling, discrete sampling).

Definitions used:

Prey types – e.g. teleost fish, cephalopods, crustaceans, elasmobranches, seabirds, “other”

Prey group – lowest possible taxon to which prey within any prey type were identified (i.e. includes at the species or genus level, or higher)

Sample – all the scats collected during a sampling occasion

Pooled sample – a sample of scats for which all the individual scats collected were pooled together in a single container

Discrete sample – a sample of scats for which all the individual scats collected were kept separately of one another

Diagnostic prey structure – undigested prey remain found in scat material that is useful for identification

4.2 Collecting scats

- Ideally scats should be collected fresh, but sufficient fresh scats may not be available. Scats showing outward desiccation are probably less than five days old if the core is still dark. Their inclusion in samples leads to representation of diet within approximately one week prior to collection (Jean-Paul Roux pers. comm.), considering that experiments in captivity have shown that all otoliths are evacuated within 24 hours (Millar 1996);
- Care should be taken to avoid inclusion of significant amounts of material from the substratum on which scats are found;
- For the sake of hygiene, rubber gloves should be worn for handling the scats;
- Samples must be labelled with the date and location of sampling (it is recommended that good quality paper tags are used, inscribed with a soft lead pencil);
- Samples should be sealed after collection, with the label inside the container;
- Unless a sample is processed soon after analysis, it should be frozen until such time it can be processed;
- To moderate disturbance to the colony, the fieldworker(s) should attempt to move slowly and avoid silhouetting themselves in the seals' line of vision (e.g. by approaching upright over elevations in the colony). Approaching with the wind from behind is not recommended as human scent frequently causes seals to stampede.

4.3 Sampling design

The sampling protocol should be determined by objectives of the study, taking into account the levels of reliability or precision required, and logistic constraints.

4.3.1 Manner of sampling – pooled versus discrete samples

Scats may be placed together in a single container (e.g. packet or bucket) as they are collected (pooled sample), or each scat may be placed in a separate container (discrete sample). The sample is defined here as all the scats collected during a sampling occasion, but in the former case, scats are indistinguishable from each other after collection (i.e., they are treated as a single scat), whereas in the latter case, scats may be analysed independently of each other.

Probably the most important shortcoming of pooled samples, compared with discrete samples, is that a single scat containing anomalously high numbers of prey structures of one or more species can significantly skew abundance and mass estimates of prey in the former. In a discrete sample, such effects are moderated as abundance and mass are statistically estimated from all the scats in the sample, each of which is assigned equal importance and assumed to be independent of all other scats in the sample. In a pooled sample, it is each prey individual (represented by one or more diagnostic prey structures) that is assigned equal importance and assumed to be independent of all other individuals. From this perspective, use of pooled samples may inherently assume an incorrect paradigm with regard to the foraging behaviour of Cape fur seals, considering that prey which display shoaling behaviour comprise the bulk of their diet (Mecenero 2005) and shoaling individuals are not independent of each other. Finally, a discrete sample allows for calculation of frequency of occurrence (FO), and of variability in estimates of numerical abundance (N) and estimated mass (M) (see Section 4.6.2 for explanations of these measures) of prey groups, whereas a pooled sample does not.

An advantage of pooled samples over discrete samples is that incomplete scats or fragments can be included. For discrete samples each individual scat is assigned equal importance therefore scats should be collected in their entirety. However, scats are not always found in discrete units – seals may defecate while in motion resulting in spreading, scats may disintegrate as a result of physical forces, or they may be accumulated along the shoreline by wave action prior to collection. Attempting to collect discrete units may therefore result in bias towards scats that are less prone to disintegration due to their size (causing possible bias in favour of larger animals) or consistency (causing possible bias in favour of certain diets).

Furthermore, from a practical perspective, processing a sample of discrete scats is far more time consuming than processing a pooled sample containing a similar number of scats. Due to this constraint, pooled sampling is currently the *modus operandi* for the ongoing diet monitoring study in Namibia (National Marine Information and Research Centre (NATMIRC) unpubl. data). By duplicating pooled samples, i.e. by collecting two samples at the same time with similar numbers of scats, some indication of the precision of estimates can be obtained.

4.3.2 Frequency of sampling

The temporal pattern in the diet of Cape fur seals at discrete locations has been shown to be unpredictable both between and within years (Mecenero *et al.* 2006b). Occasional and/or sporadic sampling is therefore inadequate for assessing diet and tracking shifts therein. Mecenero (2005) found that samples collected once-monthly was sufficient to describe the temporal heterogeneity in the relative abundance and mass of the major prey groups in the scats, and recommended that sampling be conducted on the same date each month. However, more frequent sampling (e.g. every 2 weeks) may be desirable, if for instance an aim is to estimate fish growth from otoliths found in the scats (e.g. Roux 2007), or to complement other studies (e.g. satellite telemetric studies on at-sea movements) with dietary information (e.g. Guinet *et al.* 2001).

4.3.3 Sample sizes

The question of how many scats are sufficient to assess diet and detect differences in diet geographically or over time has implications for the interpretation of results (Trites and Joy 2005). If too few scats are collected, inaccurate conclusions might be made, if too many are collected, time and financial resources may be wasted (though less so in the case of pooled samples).

Through repeated random sampling of data derived from discrete samples of Cape fur seal scats, Mecenero (2005) determined 95 % confidence intervals (CI) around statistics quantifying each prey group (FO, N, M). The maximum widths of the 95 % CI's obtained for each measure, after random sampling of prey combinations at various sample sizes of scats, are shown in Table 1. The table indicates that for a sample size of 90, the widths of the CI's around each of the three statistics under consideration did not exceed 20 % for any combination of prey. Studies further afield have also shown that close to 100 scats should be collected to be able to make adequate comparisons between occasions or between locations (Hammond and Rothery 1996, Trites and Joy 2005). However, it must be considered that the sample used by Mecenero (2005) in the randomization and bootstrapping procedure was heterogeneous, as it was necessary to draw from scats collected at three different colonies over two years (mainly at monthly intervals) to achieve sufficient combinations for bootstrapping. Considering that diet varies between locations, seasons and years (Mecenero *et al.* 2006a, 2006b), it is probable that the CI's thus obtained are over-inflated, and that lower sample sizes than those specified in Table 1 are adequate to achieve a given level of reliability in estimates.

In many cases, it may be necessary to compromise desired sample sizes on account of practical constraints, such as the availability of scats in the colony or the time/manpower available to process and analyse them. The degree of disturbance caused by collecting a large number of scats, may also be a consideration.

Considering the above, it is recommended that if discrete sampling is employed, at least 40 scats (at which sample size the CI widths around the estimates of prey groups should not exceed 30 % for any of the measures according to Table 1) should be collected per sampling occasion. However, it is recommended that the effect of sample size on the reliability of estimates needs to be re-visited, using a more homogeneous sample (i.e., numerous scats collected at one location within a short interval of time) to inform guidelines for future sampling.

By analysing duplicate pooled samples (collected at the same colony on the same day) and conducting pair-wise comparisons of the % N of each prey group between the samples, it has been shown that 35–55 scats in a pooled sample yield results within 15 % of each other for most prey groups (NATMIRC unpubl. data). Therefore, as for discrete samples, it is recommended that at least about 40 scats be collected per pooled sample (collection of duplicate pooled samples is recommended, so that the precision in estimates can be verified).

4.3.4 Other considerations for sampling

If the foraging behaviour (prey preferences, at-sea distributions) of all the individuals comprising the foraging population of a seal colony were similar, and all were equally likely to deposit scats in the colony, it could be assumed that scats collected randomly on any occasion were representative of the foraging population. However, foraging behaviour and the timing and frequency of bouts ashore vary with the sex and age of individuals (Chapter 5). Furthermore, the spatial distribution of the population ashore at any given time is unlikely to be random in terms of sex-age structure (Rand 1967). Considering that the age and sex of animals from which the scats came are not known with certainty, these dynamics need to be taken into account in any sampling design.

Some studies (e.g. de Bruyn *et al.* 2003, Mecenero *et al.* 2006a) assumed that all scats collected at breeding colonies were deposited by adult females, which comprise the bulk of the seal numbers older than pups (which are lactating) at these colonies throughout most of the year. If, as in these studies, the diet of a particular component of the population is of interest, care should be taken to exclude any portion of the colony with significant numbers of other sex- or sex-age classes (e.g. males).

4.4 Preparation of scats for analysis

- Scats should be soaked for a few hours (or overnight) in a solution of one part liquid detergent to 100 parts water, in a bucket or jar. The detergent is not essential, but facilitates the separation and cleaning of hard parts;
- With the aid of running water, the mixture must be passed through nested stainless steel sieves. Mecenero (2005) used sieves with apertures of 2.0, 1.0, 0.425 and 0.212 mm, for large, pooled samples. The smallest mesh size should not allow the smallest structures to pass through. For small, discrete samples, only one sieve may be necessary (0.212 mm);
- Keeping the material collected in different sieves separate facilitates the extraction of diagnostic prey structures.

As an alternative to sieves, otoliths can be collected by washing off other material or “panning”, because they are denser than most other structures. However, this can result in other useful prey remains (e.g. cephalopod beaks) being lost unless washed off material is retained somehow.

4.5 Analysis

4.5.1 Extraction and sorting of diagnostic prey structures

- Following washing, wet scat material should be placed on paper towels over a flat surface to dry;
- The material may be air dried, but this is time consuming and not recommended for large samples. Alternatively, material can be dried in an oven set at no more than 50℃ (otoliths may disintegrate at higher temperatu res);
- Dried material should be stored in appropriately labelled plastic bags until such time they can be sorted;

- After drying, cephalopod beaks should be re-hydrated prior to identification and measurement;
- Before sorting, the dried material must be placed on a sorting board. The sorting board should have a hard, smooth even surface (e.g. a large tray or a glass/perspex pane). Ideally, the surface of the sorting board should be of a dark colour. This can be achieved by painting the lower surface of a transparent pane black. For large (pooled) samples, a surface size of about 70 cm * 50 cm is adequate;
- The working area should be carefully chosen, bearing in mind that gusts of wind can cause the loss of dry material from the sorting board;
- Tweezers can be used to separate prey structures from waste material;
- A strong desk lamp will aid the sorting process and ease the strain on the eyes;
- As they are extracted, similar diagnostic prey structures should be grouped together to facilitate counting and identification.

4.5.2 Identification of diagnostic prey structures

- Relatively intact material can be identified with the aid of keys (Smale *et al.* 1993) and reference material. Reference collections exist at the Port Elizabeth Museum (Bayworld), NATMIRC (Swakopmund), the Department of Environmental Affairs, branch Oceans and Coasts (Cape Town) and the Iziko South African Museum (Cape Town). Expert advice should be sought for structures that are difficult to key;
- Structures should be identified to species level where feasible;
- Voucher specimens should be retained, for confirmation of identification when expert advice is not at hand, and for future reference;
- Structures that could not be identified must be given a distinctive label (e.g. “unid. 1”, etc).

4.5.3 The usefulness of different prey structures

Seal diet is typically characterised from scats by identifying otoliths of teleost fish and beaks of cephalopods found in the scats. Sagittal otoliths are the fish structures that are most resistant to digestion and are the most easily identifiable of the structures found in scats, although some closely related fish species cannot be easily distinguished by their otoliths. The size of the sagittal otoliths is also a good predictor of fish size. The other otolith types (the lapillus and the astericus) are smaller and are rarely found in scats.

Body mass of cephalopods can be predicted from beak measurements. The lower beaks are generally less ambiguous with regard to diagnostic features than upper beaks, and are therefore more useful for identification and estimation of body mass. With appropriate correction factors, otoliths and beaks can be used to enumerate the ingestion of this prey type.

Other structures of fish such as vertebrae, dentaries, eye lenses and scales may also be found in scats. Identification of these may increase the likelihood of identifying all the prey consumed, but this would require additional time and familiarity with the morphology of fishes. Staniland (2002) reported that eye lenses of squid and fish gave a better estimate of numbers eaten than otoliths and beaks, respectively. However, information allowing for back-calculations of fish size from such structures is lacking, therefore they are useful only for estimation of FO and N. Information that can be obtained from structures such as feathers, spines and fragments of exoskeletons of other prey types that are less prevalent in the diet, are also fairly limited. In some cases, these structures may provide evidence for the size or age of prey, but generally they do not allow for enumeration of prey ingested. Such structures should be identified and recorded where possible, although their usefulness is largely qualitative.

<u>The remaining sections focus only upon the use of otoliths and beaks, for the analysis of the teleost and cephalopod components of diet</u>. These are the most important prey types in the diet of Cape fur seals (David 1987a, Lipinski and David 1990).

4.5.4 Enumeration of prey structures

- Following sorting and identification, the prey structures used to enumerate each prey group need to be counted;
- For cephalopod prey groups, upper and lower beaks must be distinguished and counted separately. The more numerous beak halves of a prey group are assumed to represent the minimum number of individuals ingested;
- Numbers of fish can be estimated for each given prey group by dividing the total number of otoliths by two, but this assumes that the probability of recovery of an otolith is independent of which side of the cranium it occurs. Alternatively, left- and right-side otoliths can be separated according to shape then counted separately, with the more numerous side taken to represent the minimum number of individuals. In

this case, if damaged or eroded otoliths that cannot be distinguished left from right are present, they can simply be divided by two with the quotient to be added to the count of left- or right-side otoliths (whichever one of these is the maximum count). Separation of left- from right-side otoliths is the most accurate approach but is the most time-consuming, especially when small shoaling fish are abundant in the sample. An even more accurate and time consuming method of determining the number of individuals represented is to pair left- and right-side otoliths of similar size;

- When prey structures of a given prey group are abundant, enumeration can be assisted with a hand-held counter.

4.5.5 Measuring of prey structures

- In the case of otoliths, potentially useful measurements include maximum length, width, thickness, weight and circumference. The measurement regarded as the best predictor of fish size is otolith diameter (OD), defined as the greatest diameter of the otolith (Smale *et al.* 1995). This is usually the distance parallel to the sulcus from the anterior to posterior margins;
- In the case of squids, rostral length (LRL) of the lower beak gives the best prediction of body mass, while the best prediction of body mass in octopods and sepioids is provided by crest length (LCL) of the lower beaks. If lower beaks are unavailable, it may be possible to derive an estimate by measuring the corresponding dimension on the upper beak and applying an appropriate correction factor (Pierce *et al.* 1991); Identification to the lowest possible taxon is essential, as relationships between size and body mass of cephalopods can differ markedly between species (Santos *et al.* 2001);
- Structures can be measured with Vernier callipers (to 0.05 mm) or, in the case of minute structures, a graticule on a light microscope;
- Where prey structures are abundant, it may be necessary to sub-sample before measuring (see Section 4.5.6);
- Also, where otoliths have been divided into left from right, it will save time to measure just the otoliths of one side. Whichever side is chosen, should be consistently measured;
- Allowance needs to be made for loss of size of structures during the digestive process (see Section 4.6.2.3).

4.5.6 Sub-sampling

Sub-sampling can be performed to reduce labour if time is limiting. That is, once structures have been extracted, sorted, identified and counted, it may be necessary to sub-sample small, numerous prey to reduce the time spent measuring. Prior to sub-sampling, it is necessary to ensure that the distribution of structures in a sample is unbiased. This is not necessarily straightforward and requires careful consideration to avoid biased sub-samples.

The variability in the size of structures of a given prey group should be considered in deciding how many to include in the sub-sample. For bag samples, Mecenero *et al.* (2006a) measured c. 30 otoliths in the case of prey groups that had low variability in otolith lengths, such as gobies (*Sufflogobius bibarbatus*) and sardines (*Sardinops sagax*). Where variability in otolith length was obviously high, as in the cases of horse mackerel (*Trachurus trachurus capensis*) and hake (*Merluccius* spp.), c. 200 otoliths were measured, if their numbers exceeded this amount. However, if an objective is to measure fish growth from otolith size, higher sample sizes are required (400–600 when available), especially when samples show bimodal distributions (Jean-Paul Roux unpubl. data).

4.6 Interpretation of diet

4.6.1 Biases of scat analysis

Interpreting the results of scat analysis is not straightforward as the method is subject to numerous biases, most of which are not independent of one another. These include the following (from Pierce and Boyle 1991, Croxall 1993, Santos *et al.* 2001):

- Otoliths or beaks of different prey groups and/or of different sized individuals may pass through the gastrointestinal tract at different rates. If all scats resulting from a meal were produced on land, this would not pose a problem. However, if scats were produced before hauling out on land (which is most likely the case), prey with more rapid passage rates would be under-represented in scats retrieved from the colony. In this case, small fish and cephalopods are likely to be under-represented and cephalopods, which are prone to retention in the stomach rugae because of their irregular shapes, may be over-represented compared with fish;

- Some prey structures (especially smaller, more fragile structures) may be completely digested in the gastrointestinal tract, and therefore under-represented in the scats compared to larger, more robust structures;
- Prey structures may be reduced in size by digestion, resulting in underestimates of back-calculated prey sizes;
- Seals may fragment large prey and discard portions, such as the heads of fish, causing loss of identifiable remains and consequently, under-representation in the scats of the prey groups concerned;
- Regurgitation of indigestible remains such as cephalopod beaks will result in their under-representation in scats;
- It is possible that structures of secondarily ingested prey (i.e., prey occurring in the gastrointestinal tract of a seal's prey) may "contaminate" samples;
- Prey groups with small and fragile hard parts are more likely to go undetected in the scats.

4.6.2 Analytical techniques for describing diet composition

4.6.2.1 Frequency of occurrence

FO can be defined as the number of scats within a sample in which a given prey group is represented. Consequently, this technique is most applicable to discrete samples. FO is usually expressed as a percentage of the number of scats in a sample. The % FO of each prey group i in a discrete sample j (% FO_{ij}) consisting of k scats, can be expressed as

$$\%FO_{ij} = \frac{\sum_{j=1}^{k} p_{ij}}{} \times 100 \tag{1}$$

where $p_{ij} = 1$ if scat j contained prey group i, $p_{ij} = 0$ otherwise. As most scats will contain more than one prey group, the % FO values of the prey group present in a sample will sum to more than 100 %. This can be overcome by adjusting the % FO of each prey group present so that the adjusted percentages sum to 100 %. Bigg and Perez (1985) termed this estimate the "modified FO".

FO is a qualitative technique which, through disregarding prey size and numbers, exaggerates the importance of minor prey that is consumed incidentally. For this reason, FO on its own is not an adequate means of representing diet composition, and whenever possible, additional information from counts and measurements of prey should be utilised (Croxall 1993). Nevertheless, FO may be useful for addressing certain questions, such as the presence in the diet of prey types such as crustaceans and seabirds which do not lend themselves to the quantification of N or M (Mecenero *et al*. 2006c).

4.6.2.2 Numerical abundance

N represents the numbers of individuals counted per prey group. The counts for each sample need to be standardised for comparison, therefore they are usually expressed as % N. Depending on the motives of the study, it may be necessary to first correct the counts for numbers lost during digestion. Uncorrected counts, representing the minimum number of the different prey present, may be adequate for spatial or temporal comparisons to detect variation in diet. However, attempting to estimate diet composition and consumption requires that allowance be made for the loss of prey structures. Correction factors have been derived for some important teleost prey groups based on captive feeding experiments where the output of diagnostic prey structures in the scats was compared to their input. These prey groups include hakes, horse mackerel, goby and sardines (see Table 2). The correction factors should be applied to the number of individuals counted per scat (or pooled sample). In the case of teleost prey groups for which no correction factor has been estimated (including unidentified prey groups) Mecenero *et al.* (2006a) applied the correction factor of whichever of the above prey groups had the most closely resembling otoliths, in terms of size and characteristics, to the prey group in question (see Table 2). E.g. the correction factor for sardine was applied to round herring (*Etrumeus whiteheadii*) and anchovy (*Engraulis encrasicolus*), and that of goby to myctophid spp. However, inferring relationships derived from other prey groups may simply increase errors in abundance estimates. For instance, recovery rates of cephalopod beaks are known to be negatively related to size (Staniland 2002), thus a correction factor derived for one group may be irrelevant for many other cephalopod prey groups. Clearly, more research into determining the rate of loss of prey structures are needed, to reduce errors in estimates of abundance.

The % N of prey group i in a pooled sample p ($\%N_{ip}$) is

$$\%N_{ip} = \frac{n_i}{n_j} \times 100 \qquad (2)$$

where n_i is the number of individuals of prey group i in the sample and n_j is the number of individuals of all prey groups in the sample. Where correction factors have been applied, N and n are substituted by N* and n*, the corrected numbers of otoliths, in the above formulae. The % N of each prey group i in a discrete sample j (% N_{ij}) consisting of k scats, can be determined is then

$$\%N_{ij} = \sum_{j=1}^{k} \frac{n_{ij}}{n_j} \times 100 \qquad (3)$$

where n_{ij} is the number of individuals of prey group i in scat j (j = 1, 2, …, k), and n_j is the number of individuals of all prey groups in scat j. The variance of % N_{ij} is

$$\sigma^2\left(\%N_{ij}\right) = \frac{\sum_{j=1}^{k}\left[\left(\frac{n_{ij}}{n_j} \times 100\right) - \left(\frac{\sum_{j=1}^{k} \frac{n_{ij}}{n_j}}{k} \times 100\right)\right]^2}{(k-1)} \qquad (4)$$

4.6.2.3 Mass (M)

Describing diet composition by numerical abundance is likely to over-emphasise the importance of small prey to the diet, as the size of prey is not taken into account. Estimating the mass of prey at the time of ingestion from measurements of prey structures, may render a more meaningful picture of diet composition, especially where prey stock assessment or management is involved (Croxall 1993).

Regression methods exist for back-calculating fish length from otolith length for many of the prey species of the Cape fur seal. Fish mass may then be derived from regressions of fish length to fish mass. Where available, regressions from local fisheries data should be used, since this relationship varies regionally and seasonally (Pierce and Boyle 1991). Otolith- to fish-length, and fish length- to mass regressions used by Mecenero *et al.* (2006a) are given in Table 2. For those species for which such relationships had not yet been derived, Mecenero *et al.* (2006a) assigned regressions of closely related species. Regressions for cephalopods are supplied by Clarke (1986).

In the case of cephalopods, beaks that are recovered from scat material in one piece show negligible reduction in the size of the dimensions of interest (Harvey 1989).

However, back-calculation of fish size from eroded otoliths can introduce considerable errors in estimates of diet composition. This source of error can be addressed either by measuring only otoliths that are apparently un-eroded (i.e. retaining all, or nearly all, of their surface characteristics), or applying correction factors derived from captive feeding experiments that compare the size of prey structures before ingestion and after ejection. According to Pierce and Boyle (1991), the first approach is subjective and may bias findings towards fish with more robust otoliths.

Factors that take erosion into account that can be applied to the measured otolith diameters to obtain corrected otolith sizes, have been determined for some important prey groups, including hakes, horse mackerel, sardine and goby (see Table 2). In the case of unidentified prey groups, or prey groups for which no correction factor has been determined, Mecenero *et al.* (2006a) used the correction factor of whichever of the above prey groups had otoliths that corresponded most closely with the prey group in question, in terms of size and characteristics (as for the estimation of corrected N, above).

The % M of prey group i in a pooled sample p (% M_{ip}) is

$$\%M_{ip} = \frac{m_i}{m_j} \times 100 \qquad (5)$$

where m_i is the mass of prey group i in the sample and m_j is the mass of all prey groups in the sample; m_{ij} is the product of n_{ij} (or n^*_{ij}) and mean prey size (grams) back-calculated from the relevant prey structures; m_i is the product of n_i (or n^*_i) and mean prey size (grams) back-calculated from the relevant prey structures. The % M of each prey group i in a discrete sample j (% M_{ij}) consisting of k scats, can be determined is

$$\%M_{ij} = \frac{\sum_{j=1}^{k} \frac{m_{ij}}{m_j}}{} \times 100 \qquad (6)$$

where m_{ij} is the mass of prey group i in scat j (j = 1, 2, …, k), and m_j is the mass of all prey groups in scat j. The variance of % M_{ij} is

$$\sigma^2\left(\%M_{ij}\right)=\frac{\sum_{j=1}^{k}\left[\left(\frac{m_{ij}}{m_j}\times 100\right)-\left(\frac{\sum_{j=1}^{k}\frac{m_{ij}}{m_j}}{k}\times 100\right)\right]^2}{(k-1)} \tag{7}$$

4.7 Preservation of extracted prey structures

- Fish otoliths (and other bones) are dissolved by formalin and are also affected to some extent by alcohol. They are best preserved dry, e.g. in plastic vials;
- Structures of other prey types (e.g. cephalopod beaks, cartilaginous material) deteriorate if stored dry, and should be preserved in 70 % ethanol. If preserved in formalin, it should be no stronger than a 4 % solution, and they should be re-hydrated in 70 % ethanol at least three days prior to identification and measuring, to prevent biases (Clarke 1986).

Table 1 Maximum confidence intervals obtained for the means of % FO, % N and % M, of prey groups in discrete samples of scats, after random sampling of various prey combinations at a range of sample sizes (numbers of scats). Adapted from Mecenero (2005).

No. of scats	Maximum CI width		
	% FO	% N	% M
10	60.0	59.7	45.0
20	40.0	40.0	33.1
30	33.3	33.5	25.0
40	30.0	28.4	22.4
50	28.0	24.1	19.7
60	25.0	22.5	18.9
70	22.9	20.3	18.0
80	22.5	18.8	17.0
90	20.0	17.2	15.6
100	20.0	16.0	15.1
120	17.5	14.3	14.0
140	16.4	13.6	12.5
160	15.6	12.5	11.8
180	14.4	11.7	11.4
200	13.5	11.2	10.8

Table 2 Factors to correct for numbers of otoliths lost and erosion of otolith diameters during digestion, as well as equations for converting corrected otolith diameter to fish total length and mass, for teleost species in the diet of Cape fur seals. Family, species and common names are given. Otoliths of species for which there are no correction factors or for which relationships between otolith diameter and fish length or mass were unknown, were allocated the correction factors or relationship equation of either horse mackerel (HM), hake (H), goby (G) or sardine (S) depending on otolith similarities (shape, size and thickness; see column two and five, respectively). "A" refers to anchovy and "RH" to round herring. Adapted from Mecenero *et al.* (2006a).

Prey Group Family *Species* (common name)	Correction factors			Equation values for relationships between otolith diameter and fish total length or mass				
	Prey species correction factor used	Numbers lost[1]	Otolith diameter erosion[1]	Prey species relationship used	Fish total length		Fish mass	
					a[2]	b[2]	a[2]	b[2]
1) Horse mackerel (juvenile)								
Carangidae *Trachurus trachurus capensis* (Cape horse mackerel)	HM	1.754	1.025	HM	3.3550	1.0627	0.0042[3]	3.2384[3]
2) Hake (juvenile)								
Merlucciidae *Merluccius capensis* and *M. paradoxus* (Shallow and deep water Cape hake, respectively)	H	1.515	1.073*	H	2.7273[4]	1.1691[d]	-4.1569[4]	3.6965[4]
3) Lanternfish								
Myctophidae *Lampanyctodes hectoris*	G	1.786	1.050	*L.hectoris*	3.1988	1.2676	-2.5907	4.2197
4) Goby								
Gobiidae *Sufflogobius bibarbatus* (Pelagic goby)	G	1.786	1.050	G	3.5201	1.0564	-1.1459	3.3309
5) Pelagics								
Clupeidae *Sardinops sagax* (South African sardine)	S	3.125	1.150	S	3.9583	1.0689	0.0045[3]	3.2049[3]
Engraulis encrasicolus (Cape anchovy)	S	3.125	1.150	A	3.7039	0.9137	0.0041[3]	3.1951[3]

(cont.)

Prey Group Family *Species* (common name)	Correction factors			Equation values for relationships between otolith diameter and fish total length or mass				
	Prey species correction factor used	Numbers lost[1]	Otolith diameter erosion[1]	Prey species relationship used	Fish total length		Fish mass	
					a[2]	b[2]	a[2]	b[2]
Etrumeus whiteheadii (Cape round herring)	S	3.125	1.150	RH	3.7965	1.1088	0.0047[3]	3.1002[3]
6) Others								
Albulidae								
Pterothrissus belloci (Longfin bonefish)	H	1.515	1.073*	H	2.7273	1.1691	-4.1569	3.6965
Ariidae								
Galeichthys feliceps (White barbel)	H	1.515	1.073*	*G. feliceps*	2.3402	1.4017	-4.6236	4.2773
Cynoglossidae								
Cynoglossus sp. (Sole sp.)	G	1.786	1.050	*C. capensis*	3.3518	1.3272	-2.1634	4.1337
Gempylidae								
Thyrsites atun (Snoek)	HM/H[5]	1.635	1.049	*T. atun*	3.9602	1.1198	-1.7389	3.9189
Lophiidae								
Lophius sp. (Monkfish sp.)	G	1.786	1.050	*L. vomerinus*	3.6028	1.2790	-0.3543	3.8554
Macrouridae								
Coelorinchus quadricristatus	H	1.515	1.073*	*C. simorhynchus*	2.9046	1.1803	-4.7557	3.9875
Coelorinchus sp.	H	1.515	1.073*	“	2.9046	1.1803	-4.7557	3.9875
Mugilidae								
Liza sp. (Mullet sp.)	HM/H[5]	1.635	1.049	*L. richardsonii*	2.8651	1.3398	-2.7832	3.9285
Myctophidae								
Gymnoscopelus piabilis	G	1.786	1.050	*G. piabilis*	3.2514	0.9420	-2.7910	3.1981
Lampadena luminosa	G	1.786	1.050	G	3.5201	1.0564	-1.1459	3.3309
Lampichthys procerus	G	1.786	1.050	*L. hectoris*	3.1988	1.2676	-2.5907	4.2197
Symbolophorus sp.	G	1.786	1.050	*S. boops*	3.6919	0.7005	-0.8470	2.1726

(cont.)

Prey Group Family *Species* (common name)	Correction factors			Equation values for relationships between otolith diameter and fish total length or mass				
	Prey species correction factor used	Numbers lost[1]	Otolith diameter erosion[1]	Prey species relationship used	Fish total length		Fish mass	
					a[2]	b[2]	a[2]	b[2]
Ophidiidae								
Genypterus capensis (Kingklip)	H	1.515	1.073*	*G. capensis*	2.3930	1.5630	-6.4094	5.2076
Sciaenidae								
Atractoscion aequidens (Cape salmon)	H	1.515	1.073*	*A. aequidens*	2.2440	1.4816	-4.4887	4.2412
Scorpaenidae								
Helicolenus dactylopterus (Jacopever)	H	1.515	1.073*	*H. dactylopterus*	2.6947	1.2357	-3.2748	3.8463
Soleidae								
Austroglossus microlepis (West coast sole)	G	1.786	1.050	*A. microlepis*	4.1534	1.1042	-0.0803	3.7411
Stromateidae								
Centrolophus niger (Black fish)	H	1.515	1.073*	H	2.7273	1.1691	-4.1569	3.6965
Trichiuridae								
Lepidopus caudatus (Buttersnoek)	S/HM[5]	2.440	1.088	*L. caudatus*	4.2069	1.4239	-1.9230	4.5316
Triglidae								
Chelidonichthys capensis (Cape gurnard)	G	1.786	1.050	*C. capensis*	3.6942	1.3392	-0.6257	4.1191

[1] (DL Millar *et al*, Department of Environmental Affairs unpubl. data)

[2] $\ln y = a + b \ln x$, where y = fish total length (mm) or mass (g) and x = corrected otolith diameter (mm) (Smale *et al.* 1995).

[3] $y = ax^b$, where y = mass (g) and x = total length of fish (cm); Horse mackerel: equation based on length-mass measurements made during 2000 and 2001 by NATMIRC (horse mackerel section), r = 0.99, n = 1027; Sardine, anchovy and round herring: equations determined by NATMIRC (pelagics section).

[4] Mean of *M. paradoxus* and *M. capensis*.

[5] Mean correction factor of the two species was used.

* In Namibia, 1.0586 is now used, after refining of this estimate (NATMIRC unpubl. data).

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Appendix 1

Marking of pups

Temporary marks

If the only reason for marking pups is to prevent them from being re-sampled accidentally, they can be given temporary, non-unique markers. One option is to clip some guard hairs on the top of the head or the back with curved, blunt-tipped surgical scissors. Another is to apply a little hydrogen peroxide solution (30 %) on dry or barely damp fur of either area (or both). Pups can also be marked with indelible paint (e.g. enamel paint). Hydrogen peroxide will bleach the fur a distinctive orange, although the effect will not be immediately apparent. Only a little is needed – if applied too generously it will penetrate to the skin and cause discomfit. Good quality paint is likely to wear off after 2–3 weeks, as long as the pup does not get wet before the paint is dry.

In many studies (e.g. longitudinal growth, survival) it is necessary to mark each pup uniquely so that individuals can be distinguished in future. Plastic cattle-ear tags are generally used for this. Trites (1991) found that tagging of northern fur seal *Callorhinus ursinus* pups did not affect their growth or survival, but these pups were tagged when they were between five and eight weeks of age. Tagging pups soon after birth is more likely to compromise the health of pups. Therefore, if it is necessary to mark pups individually soon after birth, it is preferable to use unique marks of a temporary nature that will not inflict injury upon the pups, and replace these at a later stage with permanent tags.

Temporary markers that have been used to identify individual pups include unique numbers bleached onto the fur of their back using hydrogen peroxide solution and a fine paintbrush (Lunn and Arnould 1997), or uniquely numbered pieces of plastic tape glued to the top of the head (Arnould *et al.* 2003). For the latter, pieces of measuring tape cut off at 1cm intervals are useful. Alternatively, the female component of flexible plastic tags can be glued to the top of the head, with the number facing upwards (Mike Meÿer pers. comm.), or else numbered pieces of Velcro can be used (Guinet *et al.* 2001). Because the pups lose their natal coat only in February–March (Rand 1956), such markers would be sufficient for a longitudinal study of growth during the first two months of life, provided they are applied correctly (e.g. the fur has to be dry if markers are stuck to the fur, and good quality glue is required).

If the pups are temporarily marked upon the head, it is advisable to have an additional mark on their lower back that may draw workers' attention if the head is concealed. A bleach mark or a paint mark could be used, although the latter may wear off after a few weeks. Likewise, if pups are uniquely bleached upon their backs with a number, bleach or a paint spot on the top of their heads would increase the chances of re-sighting them.

1. Permanent marks

If individually marked pups are required for longer study periods than two months, the study animals should be captured and tagged before they can moult off their temporary markers. A month after birth, pups are larger and more robust, and are far less likely to suffer negative effects of from tagging. Broadly, two types of tags have been used on Cape fur seals, both of which were originally designed as cattle ear tags:

2.1 Monel-metal tags

These are one-piece tags with the upper and lower faces attached to a post (the part of the tag inserted through the flipper) of rectangular cross-section. When applied, they form a flattened oval ring through the animal's flipper. Monel metal tags have the following advantages: (a) the tags are easy to apply, and (b) the tags and their inscription are long-lasting. However, they also have the following disadvantages: (a) Movement of the upper or lower part of the tag causes the whole tag, including the post, to move. As a result, high rates of loss have been reported for this tag (Shaughnessy 1994), and (b) tag inscriptions cannot be read from a distance. Binoculars are required to read them from just 3 or 4 meters away, even in good weather conditions (Gentry and Holt 1982).

2.2 Plastic tags

These have a post with a circular cross-section, and upper and lower pieces that can rotate independently when moved. Two makes of plastic tags are most commonly used for seals: Dalton tags and "Allflex" tags. Dalton Riese (soft plastic) tags have been used for Cape fur seals. Plastic tags have the following advantages: (a) they can be colour coded to distinguish year classes, (b) they are more visible than the metal tags, and inscriptions may be read from a distance – they can be read by eye from 3–5 m away (Gentry and Holt 1982), tag loss rates of plastic tags have been found to be generally lower than that of metal tags (Erickson *et al*. 1993). On the other hand, plastic tags take longer to apply than the metal tags (this is only of concern if several hundred pups have to be tagged at a time), and (b) the manufacture quality of the plastic tags used have apparently declined in recent years. Consequently, the colours of tags tend to change with time and the raised inscriptions wear away within a few years of insertion.

Tags are applied to the trailing edge of a fore-flipper, just behind the last digit, i.e. close to the body. The exact placement of the tag is important. Inserting too close to the edge increases the chance of the tag being torn out, and too close to the muscle or axilla increases the chance of infection, physical damage to the pup, and tag loss. Tagging should not be attempted by a single person. At least one extra person is required to hold the pup still and the flipper in position. Tags may also be applied to the fore-flipper between the 4th and 5th digits, buts tags are more easily torn out from this site (Gentry and Holt 1982). Spraying a mild disinfectant such as “Betadine” on the tag wounds may reduce infection and tag loss.

By double tagging pups (i.e. applying a tag in each fore-flipper), the chances of losing a pup’s identity (through tag loss) is more or less halved. Moreover, if the goal of tagging pups is to determine their survival rates, double tagging of at least a portion of the sample will be necessary to allow for estimation of tag loss rates, which may vary between left- or right-side flippers and can have a profound effect on estimates of survival if not accounted for. If it is important to be able to determine tag loss rates, it is advisable that only one person be responsible for applying the tags, as tag loss rates can vary drastically with the identity of individual taggers (Shaughnessy 1994). At least, care should be taken to standardise the procedure if there is more than one tagger, and the identity of the tagger should be recorded for each pup, to be taken into consideration when calculating tag loss rates.

ANNEX 2

Publications by SP Kirkman relating to seals

Pistorius PA, Bester MN, **Kirkman SP** (1999) Survivorship of a declining population of southern elephant seals, *Mirounga leonina*, in relation to age, sex and cohort. *Oecologia* **121**: 201–211

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Pistorius PA, Bester MN, **Kirkman SP**, Taylor FE (2001) Temporal changes in fecundity and age at sexual maturity of southern elephant seals at Marion Island. *Polar Biology* **24**: 343–348

Pistorius PA, Bester MN, **Kirkman SP**, Taylor FE (2001) Pup mortality in southern elephant seals at Marion Island. *Polar Biology* **24**: 828–831

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