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## Examining natural population growth from near extinction: the case of the Antarctic fur seal at the South Shetlands, Antarctica

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**Abstract** This study examined the recovery process of an Antarctic fur-seal population, starting from minimal numbers after commercial exploitation to the now largest breeding population in the South Shetland Archipelago, Cape Shirreff and San Telmo Islets. It used direct census data from 20 breeding seasons (including 11 consecutive years) that spanned over 45 years. Since early population estimates, pup production increased at an intrinsic rate of ca. 20% which, during the last decade, dramatically slowed to 4.6%. The population-change trajectory is currently converging into a tightly bounded oscillation around an apparent equilibrium (carrying capacity), which is an order of magnitude lower than those levels before exploitation began. This pattern suggests the onset of an alternative stable state and highlights the far-reaching implications of strong and large-scale perturbations on marine systems.

**Keywords** *Arctocephalus gazella* · Population recovery · Time series · Monitoring · Exploitation · Carrying capacity

### Introduction

After the extensive commercial exploitation to which the Antarctic fur seal, *Arctocephalus gazella*, was subjected during the nineteenth Century (Bonner 1968), which left its populations near the verge of extinction, there has been a substantial recovery of this species throughout

the twentieth and early twenty-first centuries (Bonner 1968; Laws 1973; Payne 1977; Aguayo and Torres 1993; Boyd 1993). Fundamental to this recovery process were the international conservation measures adopted by the Antarctic Treaty through the advice of the Scientific Committee on Antarctic Research (SCAR) and the subsequent implementation of the Convention for the Conservation of Antarctic Seals (CCAS).

During the last five decades, numerous authors have investigated and described the population dynamics of *A. gazella* at various breeding grounds in Antarctic and subantarctic islands, starting from very reduced numbers in the initial years, to current self-sustaining populations (e.g. Bonner 1968; Payne 1977; Croxall et al. 1988; Bengtson et al. 1990; Shaughnessy and Goldsworthy 1990; Wilkinson and Bester 1990; Boyd 1993; Guinet et al. 1994; Boyd et al. 1995; Hofmeyr et al. 1997; Boveng et al. 1998; Shaughnessy et al. 1998). However, little is known of what happened after the exploitation period to the population of *A. gazella* inhabiting the Antarctic Peninsula region, particularly, the South Shetland Archipelago.

Upon discovering the South Shetlands in 1819, there were substantial colonies of fur seals throughout the archipelago. Within a few months after discovery, these islands were the scene of intensive sealing activities until about 1825. Sealers' refuges were erected along the western shores of Livingston Island, with those on the south coast being occupied mainly by North American sealers, and those on the north coast by British sealers (Stackpole 1955). After removing the coarse hair from the skin, fur-seal pelts were readily sold in London and China for clothing and making hats. The outcome of the sealing activities during the 1820s, and later during the 1870s, was the near-extirmination of fur seals from the entire archipelago. Remnant *A. gazella* individuals were not observed again in the South Shetlands until 1902, when one fur seal was seen and killed on Nelson Island during the Swedish South Polar Expedition 1901–1903 (Andersson 1905). It was not until January 1958 that a small colony of 27 animals was discovered

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at Cape Shirreff, Livingston Island by H.W. Simpson (as reported by O’Gorman 1961). No evidence of breeding or the presence of pups was observed. Fergus O’Gorman (1961) confirmed this record a year later at the same place, finding one live and one dead pup. This author foresaw the importance of this site as a reproductive colony for *A. gazella* when commenting: ‘Unfortunately, it has not been possible to procure any further information on the subsequent development of this group, despite its considerable biological interest as one of the few mammal colonies where the natural growth could be studied from its inception’ (O’Gorman 1961, p 915).

Only a few years after O’Gorman’s statement, Aguayo and Torres (1967) conducted the first comprehensive aerial and ground-based census around the South Shetland Archipelago in 1965, finding reproductive groups of *A. gazella*, not only at Livingston Island, but also at Window Islet and Elephant Island. Subsequently, Laws (1973) reported population estimates for Cape Shirreff and Elephant Island during the 1970/1971 breeding season (austral summer seasons are hereafter referred to as the year in which they ended). In 1973, Cape Shirreff was surveyed again, this time including in the census the nearby San Telmo Islets population (Aguayo 1978). During the 1980s, isolated censuses were developed at Cape Shirreff and San Telmo Islets (Cattan et al. 1982; Oliva et al. 1987), while later, Bengtson et al. (1990), Croll et al. (1992) and Meyer et al. (1996) reported *A. gazella* estimates for the whole South Shetland Archipelago for the 1987, 1992 and 1996 summer seasons, respectively.

The recovery process of this species, from the verge of extinction to current self-sustaining populations, provides a unique opportunity to investigate the outcome of a strong perturbation experiment and interpret its historical significance. Thus, using the background information described above, including published and unpublished data obtained by researchers of the Instituto Antártico Chileno throughout the 1990s and early 2000s (Oliva et al. 1987; Torres 1995; Hucke-Gaete et al. 1997, 1998; Hucke-Gaete 1999, 2001), this paper provides the results of the first comprehensive analysis of *A. gazella* population dynamics in the most important breeding site of the South Shetland Archipelago, Cape Shirreff and the nearby San Telmo Islets. Considering that this area was the scene of the most intense sealing of the entire archipelago, we expect that after almost two centuries after the perturbation ended, this population should have reached a similar population size to the one before exploitation began.

## Materials and methods

### Study area

Cape Shirreff (Fig. 1) is a low, ice-free peninsula located towards the western end of the north coast of Livingston Island, South Shetland Islands, situated at 62°28’S, 60°48’W, between Barclay

Bay and Hero Bay. San Telmo Islets (Fig. 1) are the largest of a small group of ice-free rock islets, approximately 2 km west of Cape Shirreff (Anonymous 1994).

### Population estimates

Direct counts of fur seals were made from high vantage observation points and/or while walking close to the shore by two or three observers, independently recording in each count the following six categories: pup, juvenile male, juvenile female, unidentified juvenile, adult female and adult male. Given that from late-January onwards, females and pups start dispersing to inland valleys and hilltops and thus impede a reliable census, the latest census that can be carried out is from early- to mid-January, in order to have the best field data on pup production at the study area (Hucke-Gaete et al. 1997). Furthermore, censuses are not so disruptive because harem bulls become less territorial with the dispersal of harems.

Since the early censuses developed by O’Gorman, population data available for Cape Shirreff include 20 breeding seasons between 1958 and 2002 (spanning 45 years). Direct censuses of fur seals were mostly made on foot during late-December and early-January, surveying the ca. 14 km of perimeter of Cape Shirreff, counting fur seals separately on all of the 36 beaches, inland valleys and flat hill tops. While the San Telmo Islets were also mostly surveyed on foot on ten occasions between 1987 and 2002, two sea-based partial censuses were also conducted.

Given that all censuses up to the year 2000 corresponded to single counts, a protocol was developed for assessing uncertainties in the estimates (inter- and intra-observer error) during the 2001 field season. Between- and within-observer error was assessed by undertaking three repeated counts of every sex and age category on different beaches and expressed as standard deviation (SD) (following Boyd 1993).

Total population numbers reported here include the number of adult males and juveniles of a first census developed every field season in mid- to late-December (peak of the reproductive season), together with a pup count developed during mid-January (including pup mortality), which is multiplied by 2 to account for total females, given that only those mothers that are nursing their pups on-shore can be counted, while those feeding at sea are omitted. Thus, the reported estimates provide only a minimum population estimate because of the inherent bias of excluding non-reproductive females and juveniles that possibly do not remain long in the area, whereas subadult males arrive later in the season. For the reasons outlined above, pup counts are considered to be indicative of *A. gazella* population growth, and are further treated as such in this paper.

### Population modelling

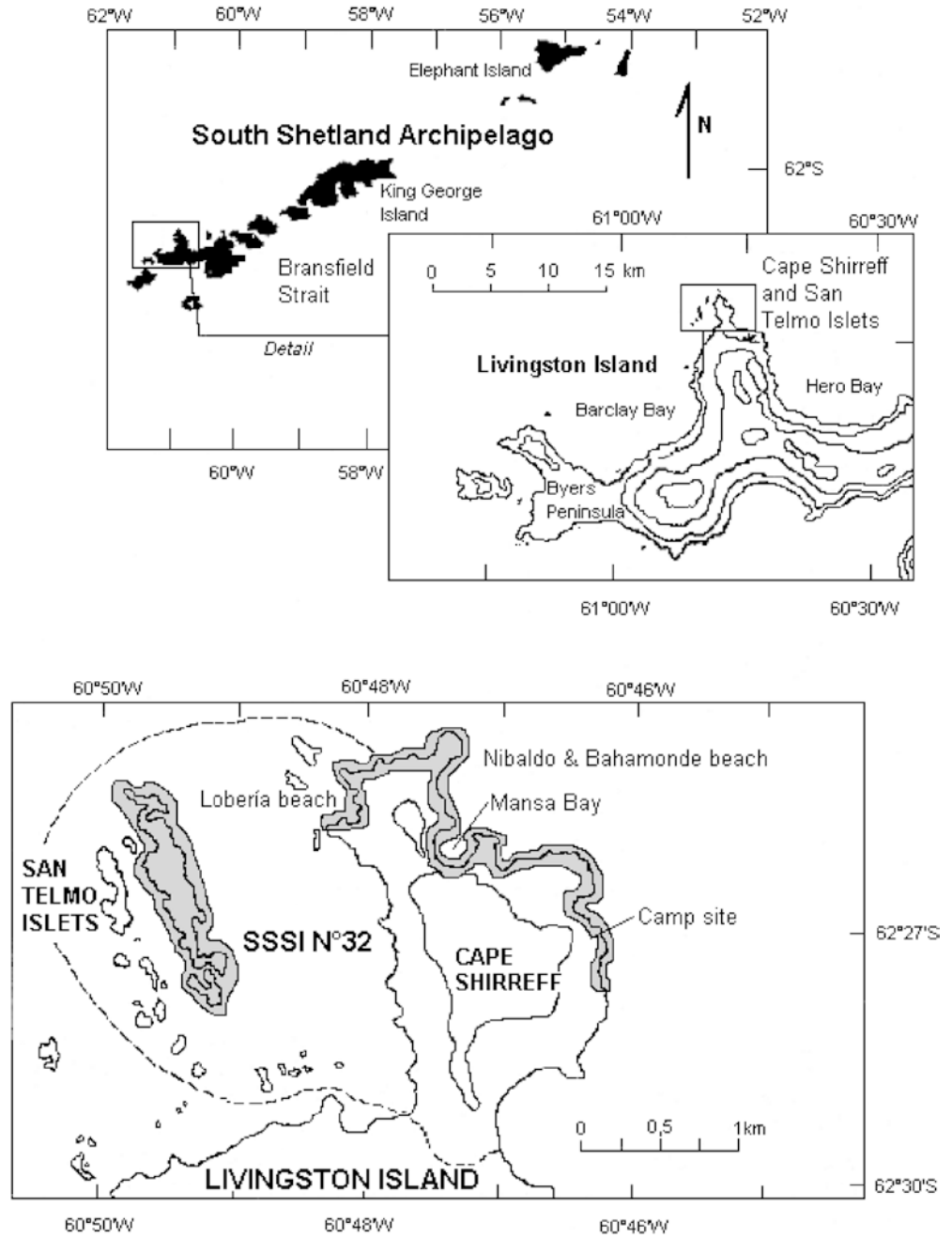
As a first step to categorize the pattern of fluctuations experienced by the population under study, the discrete form of the logistic model of population growth (Eq. 1) was fitted to the pup production series using least square regression (LSQ).

$$N_t = \frac{K}{1 + e^{-r(t-t_{50})}} \quad (1)$$

where  $N_t$  = population at time  $t$ ,  $K$  = carrying capacity,  $t$  = time elapsed at each population determination;  $t_{50}$  = year in which the population reaches  $K/2$ ,  $r$  = logistic rate constant of population change.

We use  $K$  in the sense that populations stabilize ( $N=K$ ) when the individual birth rate and death rate come to equal each other, and thus the population growth rate is zero (Wilson and Bossert 1977). This limit is expressed as a number of organisms and is an independent parameter. The logistic equation was selected as a ‘‘strategic’’ model (sensu Caughley 1977) in order to reveal the general outcome of the population growth process stripped to its essentials.

**Fig. 1** Location of Cape Shirreff and San Telmo Islets, Livingston Island, South Shetlands. The shaded area shows the current distribution of Antarctic fur-seal breeding colonies within the study area



The intrinsic ( $r_t$ ) (Eqs. 2 and 3; Caughley 1977) and finite ( $\lambda_t$ ) (Eq. 4; Caughley 1977) rates of increase were calculated for the *A. gazella* population over the period 1965/1966–2000/2001 by using the following formulas:

$$e^{r_t} = \lambda \tag{2}$$

$$r_t = \ln e^{r_t} \tag{3}$$

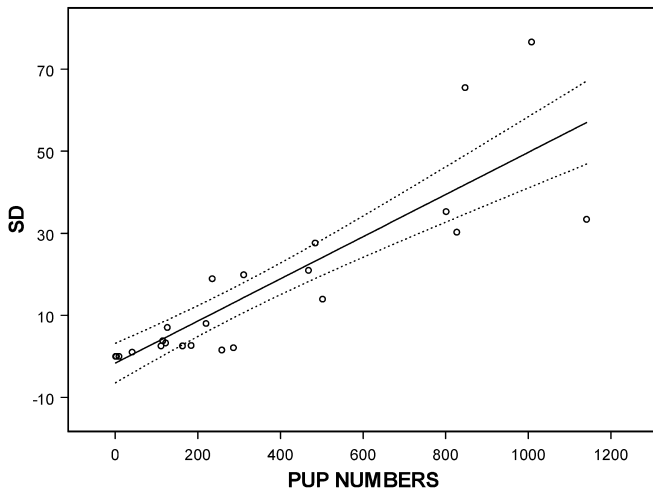
$$\lambda_t = \frac{N_{t+1}}{N_t} \tag{4}$$

The finite rate of increase can be expressed as a percentage in order to facilitate between-year and between-population comparisons. The conversion can be done by subtracting 1 from  $\lambda$  and then multiplying this value by 100 (Caughley 1977). The inflection point of the growth curve (i.e. when population growth rate declines) was identified at  $K/2$ .

## Results

The analysis of census error at both sites indicates that total inter-observer error is low (mean 3%). Outliers suggest that some factors other than density are influencing precision of censuses on some beaches (Fig. 2); however, censuses up to the present can be considered to be quite reliable and indicative of population dynamics.

The fur-seal population at Cape Shirreff increased from 11 animals counted in 1959 (including only 2 pups) (O’Gorman 1961) to 14,842 estimated in 2002 ( $r_t = 18.2\%$ ) including 6,453 pups ( $r_t = 20.7\%$ ). Data available for

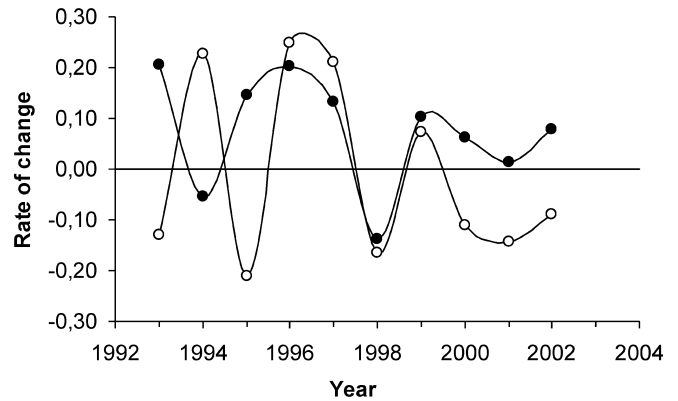


**Fig. 2** Standard deviation (SD) of Antarctic fur-seal pup counts as a function of pup numbers ( $r^2 = 0.7721$ ). The fitted linear regression (solid line) is calculated from:  $SD = 1.6682 + 0.0514 * \text{Pup Numbers}$ . Also shown is the 95% CI for the regression (broken lines)

San Telmo Islets, however, are more limited due to accessibility, and span only from 1987 to 2002. The first census that included information from San Telmo Islets, separately from Cape Shirreff, was conducted during the 1987 season, and later reported by Bengtson et al. (1990). They counted 5,781 animals (including 1,875 pups) and indicated that the population breeding there was twice the size of that breeding at Cape Shirreff. However, when the next full census was developed at both sites (1992), Cape Shirreff's population had surpassed the number of fur seals breeding at the islets, and this difference has been maintained from that year since. In 2002, the local population breeding at San Telmo Islets reached 6,348 animals ( $r_i = 0.6\%$ ), including 2,124 pups ( $r_i = 0.8\%$ ). Although no adequate density estimates (animals/m<sup>2</sup>) are currently available, simple observation suggests that San Telmo Islets shelter a much larger number of animals per unit area than Cape Shirreff.

The nature of population variation between Cape Shirreff and San Telmo Islets seems to fluctuate considerably between sites in the initial years of the time series (Fig. 3). During the early 1990s, when Cape Shirreff's population growth rate was positive (growth), San Telmo Islets presented negative values (decline), and vice versa, indicating that exchange between sites may occur inter-annually. However, during the last 7-year time series, both local populations couple their fluctuations and seem to behave in a similar way. Although the initial behaviour (3 years) is rather difficult to interpret, the overall and latter dynamics tend to support the hypothesis of Aguayo and Torres (1993), when suggesting that both sites should be treated as one population and analysed accordingly.

Between 1966 and 2002 (36 years), the total population of *A. gazella* at Cape Shirreff and San Telmo Islets increased from 50 (Aguayo and Torres 1967) to an estimated 21,190 animals ( $r_i = 18.3\%$ ). In the same way,



**Fig. 3** Intrinsic growth rate difference for Antarctic fur-seal pup counts at Cape Shirreff (filled circles) and San Telmo Islets (unfilled circles) between 1993 and 2002

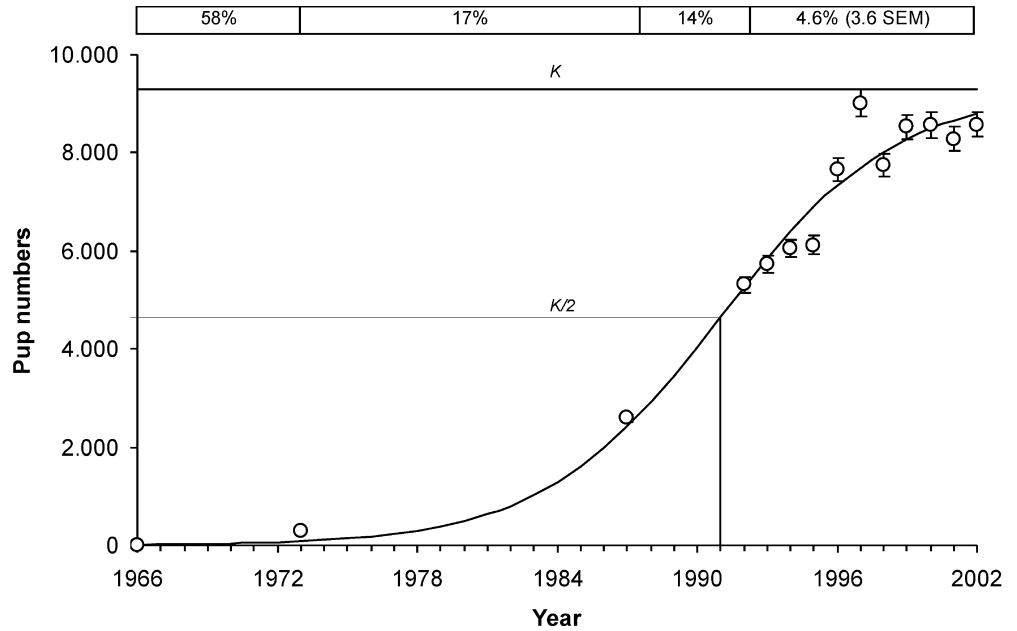
pup production increased from 12 (Aguayo and Torres 1967) to 8,577 pups ( $r_i = 20\%$ ) (Fig. 4).

Considering the historical accounts given by O'Gorman (1961) and Stackpole (1955), Cape Shirreff seems to have been a very important site for sealers. Some 95,000 fur-seal skins were reported taken by 5 British crews during the summer season of 1821/1822 (O'Gorman 1961). About 60–75 men were living ashore at Cape Shirreff in January 1821 (Stackpole 1955), and more than 90 ships were engaged in sealing activities in the area between 1819 and 1822 (O'Gorman 1961). Although the accuracy of these figures is unknown, this scenario implies that there was a substantial population in the area before sealing began. Since only adult, subadult and juvenile individuals were culled in those days (McCann and Doig 1987), a conservative pre-exploitation population estimate can be calculated by using the mean adult:pup ratio observed at both sites during the 1990s (i.e. 1.33:0.77), assuming that nearly all fur seals older than 1 year were killed. Although this approach is probably inaccurate to some degree, it is considered important since it provides an approximate figure with which to compare current population trends. Calculations using this approach suggest that the virginal breeding population of *A. gazella* might have been ca. 167,000 animals, including ca. 72,000 pups, i.e. an eightfold difference compared to the 2002 estimate (Fig. 5).

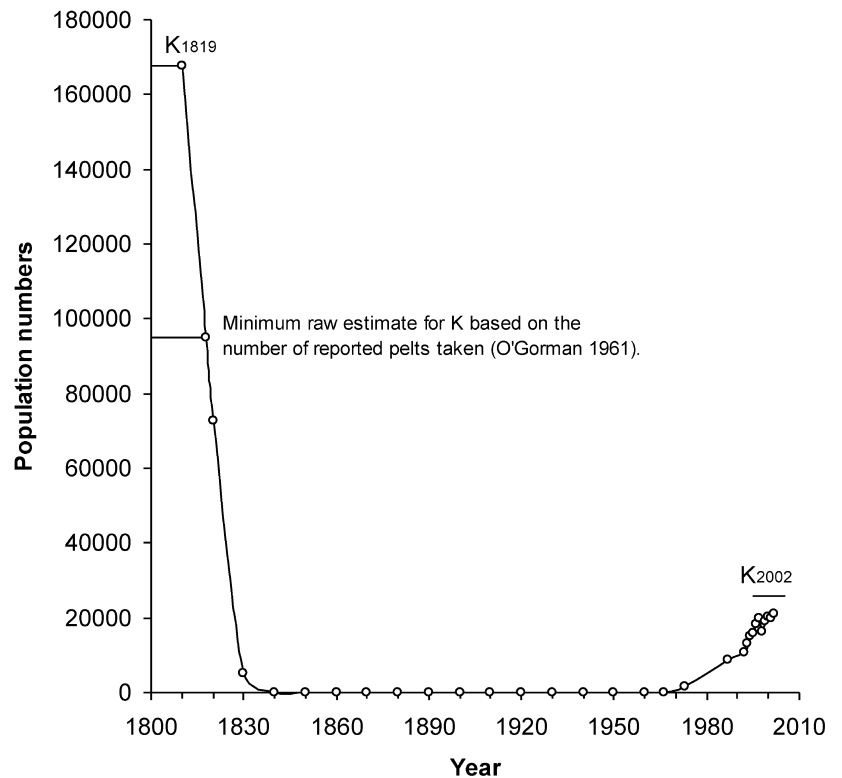
The overall population growth at the study sites had always been positive, with the exception of 1998. During that breeding season (an El Niño year), we counted 14% fewer pups than the previous year, translating this into a 16% decline in total population numbers (Hucke-Gaete et al. 1998).

The carrying capacity ( $K$ ) calculated through the logistic model reaches 9,294 pups (or a total population of 25,919 individuals including pups) and indicates that nearly 92% of the maximum sustainable density of fur seals in this particular environment has already been attained. The moment when the rate of increase starts to slow down ( $K/2$ ) was identified as having occurred during the early 1990s. At this level, half of the population that

**Fig. 4** Antarctic fur-seal pup production at Cape Shirreff and San Telmo Islets, South Shetlands (1966–2002) with 3% error bars. The *fitted line* corresponds to the logistic model parameterized by  $K=9294$ ;  $t_{50}=1991$ ;  $r=0.2625$ . Also shown in *boxes* is the percent rate of increase for different periods and the standard error of the mean (*SEM*) for the series ranging from 1992 to 2002



**Fig. 5** Antarctic fur-seal pre-exploitation and current population numbers at Cape Shirreff. Note the order of magnitude difference between virginal and present population levels [and associated carrying capacities ( $K_t$ )]. These  $K_s$  correspond to total population estimates for both historical and present periods (see Discussion for further explanations)



can be sustained by the environment has been attained and growth rate slows down, and from 1996 onwards has been close to zero [mean =  $2.5 \pm 12.5$  (95% C.I.)] (Fig. 4).

**Discussion**

Population modelling

Although the logistic model used in this study is of a simple nature, it has been helpful to explain current

trends in growth rates. The scatter in the data also implies that a more complicated model than the one used here is not justified, and in the absence of other information, the logistic is to be preferred because of its simplicity alone (principle of parsimony). However, in order to identify which factor(s) determine population dynamics, a switch to a process-based model that encompasses relevant factors will be fundamental in order to further understand the population dynamics of *A. gazella* at the study site and investigate the forces

**Table 1** Antarctic fur-seal population growth rates at different breeding locations

Location	Period	Pup production growth rate	Total population growth rate	Reference
Livingston Island	1966–1973	+ 58.4%	+ 66.1%	This study
	1973–1987	+ 16.7%	+ 12.4%	
	1987–1993	+ 14.1%	+ 6.8%	
	1993–2002	+ 4.6%	+ 5.4%	
	1966–2002	+ 20%	+ 18.3%	
South Georgia	1958–1971	-	+ 16.8%	Payne (1977)
	1972–1978	-	+ 4–5%	Boyd et al. (1990)
	1977–1991	-	+ 9.8%	Boyd (1993)
	1991–2000	-	+ 6% to + 14%	SSG (2000)
Bouvetøya	1979–1999	-	+ 14%	Calculated from Kirkman et al. (2000)
Marion Island	1989–1995	-	+ 17%	Hofmeyr et al. (1997)
Ile de la Possession (Iles Crozet)	1983–1992	-	+ 21.4%	Guinet et al. (1994)
	1992–1999	-	+ 16.9%	SSG (2000)
Heard Island	1963–1988	+ 21%	+ 23%	Shaughnessy and Goldsworthy (1990)
	1987–1992	+ 6.7%	-	Shaughnessy et al. (1998)

responsible for fluctuation in this large mammal population.

#### Population growth at Cape Shirreff and San Telmo Islets and comparison with other rookeries

The growth of *A. gazella* populations during the twentieth century has been considered as one of the most rapid population increases of any marine mammal (Laws 1984). Population growth rates for *A. gazella* in our study area between 1966 and 2002 are similar to those reported for other locations (Table 1). However, if we only consider the growth rate attained between 1965 and the year in which  $K/2$  was attained (when population growth was in its exponential phase), the rates of increase reach 23% for the total population, and 26% for pup production, and become the fastest rates reported to date. The fact that *A. gazella* populations at the South Shetlands were growing at a very high rate led Bonner (1968), Laws (1973) and Aguayo (1978) to suggest that this occurrence was due to immigration from the growing population of South Georgia. This is supported by the biologically unattainable high rate of increase observed at the study area in the early years (Fig. 4) and by the several resightings of animals marked as pups at other localities (such as Seal Island and South Georgia) (Bengtson et al. 1990; Torres 1991; Torres et al. 2000). The most intense immigration from other source populations to the South Shetlands should have occurred between 1965 and 1973, when the observed rate of increase was as high as 58% (Fig. 4). However, if the comparison is bounded to the regulation phase (1993–2002), both rates fall considerably and coincide with the lowest growth rates reported for the South Georgia population in recent years (Boyd et al. 1990), and suggest negative feedback processes at work (Fig. 4, Table 1).

#### Pre-exploitation levels and current trends

The excellent agreement between the data and the prediction of the model (Fig. 4), together with the decreasing growth rates and near attainment of  $K$ , suggest that the fur-seal population breeding at the study site is reaching equilibrium as it approaches the asymptote of the growth curve.

Considering that current population levels are an order of magnitude lower than pre-exploitation estimates (Fig. 4), an intriguing question arises: why is the current *A. gazella* population already approaching  $K$  (equilibrium) if, in the absence of exploitation, we would expect the population to reach or surpass previous levels?

A first hypothesis could be that high population growth rates will be achieved when optimal conditions dominate over varying periods of time, following some years when the population reaches an apparent but unstable equilibrium. This pattern might have the form of successive levels of equilibria punctuated by new levels of growth, and will become more evident if the monitoring of this population continues. This coincides with the view of Croxall et al. (1988), when indicating that populations of top predators reaching  $K$  will fluctuate appreciably and we are likely to have problems both in detecting and interpreting population trends.

The effects of environmental change on the population dynamics of different Antarctic species are another important aspect that could shed light on the current trend of *A. gazella* at our study area. Growing evidence suggests that the reproductive success of *A. gazella* (as well as other marine mammals and seabirds) varies in response to episodic environmental change (e.g. Croxall et al. 1988; Trillmich and Ono 1991). Due to their longevity, individuals of *A. gazella* might expect to encounter one or more such events during their lives, although exactly when any particular event would occur is unpredictable. Because of the rapid and seemingly

unpredictable nature of these large-scale environmental changes, if *A. gazella* and/or other species are to successfully exploit them, they must do so by either storing energy or reproducing when conditions are favourable. The above is consistent with the observed patterns of growth experienced by the *A. gazella* population at SSSI no. 32 when focusing on the apparent stability reached in the early 1990s, followed by a rapid increase between 1996 and 1997, and the attainment of a new equilibrium level during the late 1990s (Fig. 4).

Does the above mean that pre-exploitation levels (stable equilibrium) will slowly be reached through a saltatory pattern in the next 100 years or so, or that the suspected pre-exploitation levels are unlikely to be attained again as a consequence of major changes to the Southern Ocean, and will force the population to remain within the current levels, suggesting the onset of an alternative stable state?

Although both predictions seem plausible to some degree, there is more evidence supporting the latter alternative. Following the view of Bender et al. (1984), we can consider Antarctic communities to have been subject to man-induced "press" perturbations (defined as sustained alterations of species densities). These perturbations included the near-extirpation of various components of the ecosystem, namely, fur seals (*Arctocephalus* spp.), whales (*Balaenoptera* spp. and *Megaptera* sp.), marbled Notothenia (*Notothenia rossii*) and mackerel ice fish (*Champsocephalus gunnari*) (Agnew and Nicol 1996). This type of perturbation usually induces the community to reach new levels of equilibrium, and we propose that this is what we are evidencing in the South Shetlands area. This shift into a new level of equilibrium might be a response to the extensive exploitation regimes to which Antarctic marine living resources were subjected, and this study supports this view. Because of the above, and although the perturbation on the community has been released to a large extent, the *A. gazella* population under study (and possibly other species as well) is unlikely to reach pre-exploitation levels again unless a major perturbation changes conditions. This is further supported by the extensive growth of the *A. gazella* population at South Georgia, which is thought to have surpassed pre-exploitation levels (SSG 2000), and thus supports our view in that a new equilibrium level was attained where *A. gazella* was able to take advantage of the predominant conditions in that particular area. In the case of *A. gazella*—which not only depends on krill but also on fish for its survival (Osman 2001; Osman et al. 2004)—the depletion and delayed recovery of fish populations might have hampered its potential for growth in the South Shetlands by reducing the carrying capacity of the environment. Dietary differences between breeding locations (e.g. South Georgia) might be responsible for different carrying capacities and the differential responses of fur-seal population dynamics. The consequences of historical and more recent perturbations that have affected the structure and

functioning of Antarctic marine communities remain obscure, and in our opinion have not received enough attention.

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