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## POPULATION GROWTH OF ANTARCTIC FUR SEALS: LIMITATION BY A TOP PREDATOR, THE LEOPARD SEAL?

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**Abstract.** Antarctic fur seals (*Arctocephalus gazella*) in the South Shetland Islands are recovering from 19th-century exploitation more slowly than the main population at South Georgia. To document demographic changes associated with the recovery in the South Shetlands, we monitored fur seal abundance and reproduction in the vicinity of Elephant Island during austral summers from 1986/1987 through 1994/1995. Total births, mean and variance of birth dates, and average daily mortality rates were estimated from daily live pup counts at North Cove (NC) and North Annex (NA) colonies on Seal Island. Sightings of leopard seals (*Hydrurga leptonyx*) and incidents of leopard seal predation on fur seal pups were recorded opportunistically during daily fur seal research at both sites. High mortality of fur seal pups, attributed to predation by leopard seals frequently observed at NC, caused pup numbers to decline rapidly between January and March (i.e., prior to weaning) each year and probably caused a long-term decline in the size of that colony. The NA colony, where leopard seals were never observed, increased in size during the study. Pup mortality from causes other than leopard seal predation appeared to be similar at the two sites. The number of pups counted at four locations in the Elephant Island vicinity increased slowly, at an annual rate of 3.8%, compared to rates as high as 11% at other locations in the South Shetland Islands. Several lines of circumstantial evidence are consistent with the hypothesis that leopard seal predators limit the growth of the fur seal population in the Elephant Island area and perhaps in the broader population in the South Shetland Islands. The sustained growth of this fur seal population over many decades rules out certain predator–prey models, allowing inference about the interaction between leopard seals and fur seals even though it is less thoroughly studied than predator–prey systems of terrestrial vertebrates of the northern hemisphere. Top-down forces should be included in hypotheses for future research on the factors shaping the recovery of the fur seal population in the South Shetland Islands.

**Key words:** *Arctocephalus gazella*; *breeding chronology*; *Hydrurga leptonyx*; *mortality rate*; *population recovery*; *population growth rate*; *predation*; *pup production*; *South Shetland Islands*; *top-down limitation*.

### INTRODUCTION

Antarctic fur seals (*Arctocephalus gazella*) occupy an upper trophic position in the Antarctic marine food web, feeding mainly on krill (*Euphausia superba*) and various fish species (Croxall and Pilcher 1984, Green et al. 1989, Green et al. 1991, Reid 1995, Reid and Arnould 1996). Variability in Antarctic fur seal populations, and in populations of many other marine endotherms, has usually been associated with prey-related (“bottom-up” [e.g., Hunter and Price 1992]) forces often mediated by environmental variability (e.g., Antarctic fur seals [Boyd et al. 1994, Croxall et al. 1988], other seals [Trillmich and Ono 1991], and seabirds [Croxall et al. 1988, Ainley et al. 1995, Monaghan

1996]). Although seals and seabirds are often considered top predators, many species are themselves preyed upon by other species of seals, killer whales, or sharks. Thus, despite the usual focus on bottom-up forces controlling seals and seabirds, there is considerable scope for top-down forces to play important roles. In this paper we examine evidence for control of an Antarctic fur seal population by leopard seals (*Hydrurga leptonyx*).

The Antarctic fur seal population in the South Shetland Islands (Fig. 1) is presently recovering from early 19th-century commercial exploitation and near extinction (O’Gorman 1961, Aguayo and Torres 1967, Bengtson et al. 1990). The number of fur seals increased from a breeding colony of as few as 32 seals at Livingston Island in 1959 (O’Gorman 1961) to a population estimated to contain 19 000 seals in 1987, when most of the breeding areas were found to be on or near Elephant, King George, and Livingston Islands (Bengtson et al. 1990). However, only the breeding colonies

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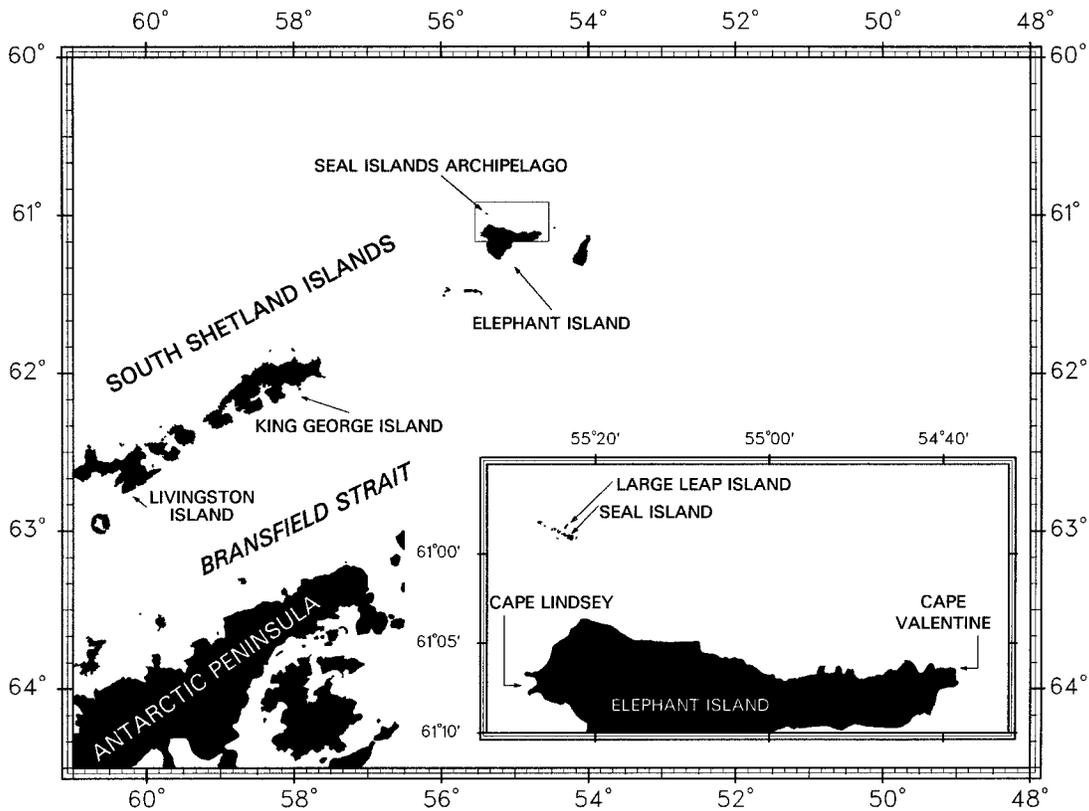


FIG. 1. Map of the northern tip of the Antarctic Peninsula, with a detail map of the Seal Islands archipelago and Elephant Island.

at Elephant and Livingston Islands have expanded since the 1960s (Aguayo 1978, Oliva et al. 1987, Bengtson et al. 1990, Aguayo and Torres 1993), indicating that the recovery of the fur seal population in the South Shetlands has been mostly limited to the vicinities of these two islands (Fig. 1). This recovery provides an opportunity to investigate the forces responsible for changes in vital rates (reproduction, mortality, immigration, and emigration) that ultimately determine the relative success of breeding colonies and the fur seal population as a whole.

To document demographic changes associated with the recovery of the subpopulation of Antarctic fur seals in the vicinity of Elephant Island, we monitored abundance and reproduction annually during austral summers from 1986/1987 to 1994/1995. This research included daily observations at two colonies in the Seal Islands (where the greatest concentration of fur seals is found), annual censuses of other colonies in the Seal Islands, and less frequent censuses of colonies on or near Elephant Island that were less easily accessible from our Seal Island field camp (Bengtson et al. 1990; Fig. 1). Because leopard seals were frequently observed at Seal Island and occasionally seen to take fur seal pups, we also documented leopard seal presence and behavior. Our objectives in this study were to: (1) de-

scribe patterns in fur seal pup production throughout the breeding seasons of 1986/1987 to 1994/1995 at Seal Island, including breeding chronology, total numbers of births, mortality rates of pups, and the effects of predation by leopard seals; (2) document abundance and trends of the Antarctic fur seal population breeding on and near Elephant Island within the larger context of the fur seal populations of the South Shetland Islands and South Georgia (1300 km east-northeast [ENE] of Elephant Island); and (3) assess the importance of predation by leopard seals in limitation or regulation of these populations.

#### METHODS

##### *Fur seal pup production and mortality at Seal Island*

We monitored pup production of Antarctic fur seals annually from 1986/1987 through 1994/1995 at Seal Island, Antarctica (60°59' S, 55°23' W, Fig. 1). Live and dead fur seal pups were counted daily or every second day from early December to early March during the 1989/1990 through 1994/1995 breeding seasons. Pups were counted less frequently or for shorter periods during the 1986/1987 through 1988/1989 seasons. Pups were usually counted between the hours of 1000 and

1600 and during low tide, if possible. Pups were counted visually by a single observer (on nine occasions when counts were replicated by independent observers, the coefficient of variation among observers was 3%). Observers counted from several vantage points affording views of each of two colonies, North Annex (NA) and North Cove (NC), which are situated in adjacent protected coves, each with a shallow lagoon connected to the open sea by two channels. The channels leading to the lagoon at NA are awash only during high tides and occasional periods of large ocean swells; the channels leading to the NC lagoon are flooded at all but the lowest tides. The breeding areas of NA and NC are ~25 m apart at their nearest points, are separated by a rock ridge that prevents overland movement of fur seals, and cover ~490 m<sup>2</sup> and 1300 m<sup>2</sup>, respectively.

We compared NA and NC because of an apparent difference in predation by leopard seals; leopard seals were seen at NC, sometimes taking fur seal pups, but they were never seen at NA. Sightings of leopard seals and incidents of leopard seal predation on fur seal pups were recorded opportunistically during daily research at NA and NC. Observer effort was not quantified, but was approximately equivalent in 1989/1990 through 1994/1995 (L. M. Hiruki et al., *unpublished manuscript*).

Pup mortality is often estimated by counting the number of dead pups seen in a pinniped colony (e.g., Doidge et al. 1984). The number of dead pups counted daily, however, may underrepresent actual pup mortality (Kovacs et al. 1985), as some carcasses may be washed away (Anderson et al. 1979) or scavenged, and some pups may be captured and removed by predators (Harcourt 1992). Furthermore, a particular pup carcass observed on one day may not be identifiable as distinct from one observed on another day without intensive efforts to mark or collect dead pups (e.g., Baker and Doidge 1984); such efforts may disturb the seal colony (Mattlin 1978). We did not mark or remove pup carcasses from the colonies, so our estimates of the cumulative number of dead pups are partly subjective, based on the observers' judgment of whether a carcass had been included in previous counts. Therefore, our serial counts of live and dead pups may not, by themselves, accurately estimate the total number of births, the chronology of births, or the pup mortality rate. To estimate those quantities from counts of live pups only, we developed a model of the chronologies of births and deaths of pups.

The model was based upon the assumptions that (1) the proportion of the pup cohort born each day is equal to the corresponding probability from a normal distribution of birth dates, (2) there was no leopard seal predation at NA, and (3) a constant fraction of the live pups dies each day from causes other than leopard seal predation (e.g., starvation, storms, or crushing by adult males). We estimated the mean and variance of the normal distribution of birth dates, the total number of

births, and the average daily mortality rate at NA in 1990/1991 through 1994/1995 using the Levenberg-Marquardt algorithm (Press et al. 1992) for nonlinear least-squares regression of pup counts vs. date. Then, assuming that the daily rate of mortality at NC from causes other than leopard seal predation was the same as the rate at NA in the same year, we estimated the mean and variance of birth dates and the total number of births at NC by the same regression model (with mortality fixed at the NA rate) using only the NC counts obtained prior to the peak count each year (there was no evidence of leopard seal predation prior to the peak counts). Extrapolating beyond the date of the peak count with these regressions provided estimates of the numbers of pups that would have been observed at NC if the overall pup mortality rate was the same there as at NA. We estimated the effect of leopard seal predation as the difference between the number of pups counted at NC at the end of each season and the number of pups predicted by the model. The number of pups dying from nonpredatory causes was estimated as the total number of births minus the estimated number of pups taken by leopard seals minus the number of live pups at the end of the season.

We could not fit the model described above to data from 1986/1987 through 1989/1990, because pup counts were initiated too late in those breeding seasons to allow reliable estimation of parameters of birth chronology and total numbers of births. Pup counts were sufficient in 1989/1990, however, to apply an approximate form of the model. To estimate the daily rate of pup mortality at NA in that year, we calculated the slope of a regression of the logarithm of NA pup counts (after 1 January, when nearly all pups had been born) as a function of date. To estimate the daily numbers of pups that would have been observed at NC in 1989/1990 if the mortality rate had been the same as at NA, we first smoothed the NC pup counts by robust locally weighted regression (Cleveland 1979). We then used the mortality rate from NA to extrapolate from the peak of the smoothed curve and compared the extrapolated pup count to the actual pup count at the end of the season, as described above, to estimate the number of pup deaths from leopard seal predation at NC in 1989/1990.

Because of serial correlation in residuals and structural correlations between model parameters, the estimates of variance typically reported by regression programs were unlikely to be reliable for our model. Therefore, we calculated precision of the model estimates by Monte Carlo simulations. Daily numbers of live pups were simulated by a stochastic version of the model, in which the probabilities of birth and death on a particular date were determined by the average estimates (across years) of mean birth date, standard deviation of birth dates, daily mortality rate, and total births. Normally distributed "counting errors" were added to these pup numbers to simulate pup counts;

the variance of the counting errors was chosen such that the variance in simulated model residuals would match the variance in the observed model residuals. For each colony, NA and NC, 1000 series of daily pup counts were simulated and the regression model described above was fit to each series. The standard deviation of the 1000 simulated estimates of each parameter was used to represent the approximate standard error for that parameter.

#### *Fur seal abundance and trends in the Elephant Island area*

In addition to the counts at colonies on Seal Island, fur seals at other colonies in the Seal Islands archipelago and at Elephant Island were counted when opportunities were available, such as during vessel operations to support the Seal Island field camp. Observers used inflatable boats to land near these colonies and visually counted all pups from vantage points or by walking slowly along the periphery of the colony. These counts were typically obtained by one or two observers; on nine occasions when pups were counted by two independent observers, the coefficient of variation between observers was 6%. Fur seal pups on the islet NNW of Seal Island, informally named Large Leap Island, were counted at least once per year from 1986/1987 to 1994/1995, usually in mid- to late January. Two smaller colonies in the Seal Islands archipelago were counted in 1993/1994 and 1994/1995. Antarctic fur seal pups in all known breeding colonies (Bengtson et al. 1990) in the Elephant Island vicinity were counted in 1991/1992 and 1993/1994.

### RESULTS

#### *Fur seal pup production and mortality at Seal Island*

Each year from early December to early January, the numbers of Antarctic fur seal pups at NA and NC colonies increased as pups were born, and then leveled off or declined as births ceased and pups succumbed to various sources of mortality for the remainder of the study season (Fig. 2). Pup counts at NA declined by <20% of their peak values, while pup counts at NC typically declined by  $\geq 50\%$  of their peak values. NC pup counts appeared to stabilize, or decline more slowly, after late January or early February. Annual peak counts of pups at NA increased by  $25 \pm 4.3\%/yr$  (mean  $\pm 1$  SE) from 1987/1988 to 1994/1995 (Fig. 3). This high rate of growth resulted mostly from the almost tripling of counts between 1987/1988 and 1989/1990, evidence for a young colony growing primarily by immigration. Pup counts at NC decreased by  $4.2 \pm 1.0\%/yr$  from 1987/1988 to 1994/1995 (Fig. 3).

From 1986/1987 to 1994/1995, leopard seals were seen 244 times at different locations around Seal Island. Of these 244 observations, 154 (63%) were between late December and late February, when pup counts at NC were declining. Leopard seals were never seen in

the lagoon at NA, possibly due to poor access to the lagoon, although they were observed on three occasions (1.2% of the total number of sightings at Seal Island) just outside the lagoon. Leopard seals were observed frequently at NC (Fig. 2; 58 sightings at NC, including three sightings of them consuming fur seal pups just outside NC), and leopard seals were seen capturing or consuming fur seal pups on 27 occasions (47% of the NC sightings). On some of these occasions, individual leopard seals captured as many as four pups during a period of  $\sim 1$  h. Leopard seals were seen in NC only after daily pup counts began to decline (the earliest sighting was on 30 December) and they were rarely seen in NC after daily pup counts had stabilized each year (the latest sighting of a leopard seal in NC was 18 February). However, leopard seals continued to be sighted elsewhere at Seal Island (35 observations, 14% of total) after pup counts stabilized. Periods when sightings of leopard seals and predation on fur seals were most frequent at NC corresponded to rapid declines in fur seal pup numbers (Fig. 2).

An example of the model results, based on counts from 1991/1992, is shown in Fig. 4. The model generally provided good fits to the pup counts: The proportion of variance in pup numbers explained by the model ranged from 0.92 to 0.99 (Table 1).

Mean dates of birth (Table 1) were, on average, 4 d later at NA than at NC. This difference was more than three times the approximate standard errors obtained by Monte Carlo simulations (1.1 d for NA and 0.66 d for NC), indicating that the breeding chronology at NA was significantly delayed with respect to that at NC. The dispersions (standard deviations) of birth dates, however, were similar between the two sites (Table 1). Approximate standard errors for that parameter were 1.2 d for NA and 0.71 d for NC, indicating that the intercolony differences (within years) were not statistically significant, except in 1992/1993 (Table 1). For that year, the estimates may not have been as precise as indicated by the Monte Carlo simulations because pup counts began relatively late (Fig. 2), and thus did not provide as much information about the chronology as in the other years.

Nine of the 10 model estimates of total births at both colonies were greater than the corresponding peak live pup counts and the estimates of total births were very close to the peak count of live pups plus the number of dead pups observed prior to the peak count (Table 1).

The estimates of mortality rates at NA from 1989/1990 to 1994/1995 indicated that  $\sim 0.3\%$  of pups died each day (Table 1), with an approximate standard error of 0.1%. Estimates of cumulative pup mortality at NA, from birth to  $\sim 75$  d of age, ranged from 16% of the cohort in 1993/1994, to 29% in 1990/1991. At NC, mortality from nonpredatory causes was similar (16–30%; Table 2), partly because the daily rate was fixed at the NA rate. The estimated proportion of pups taken

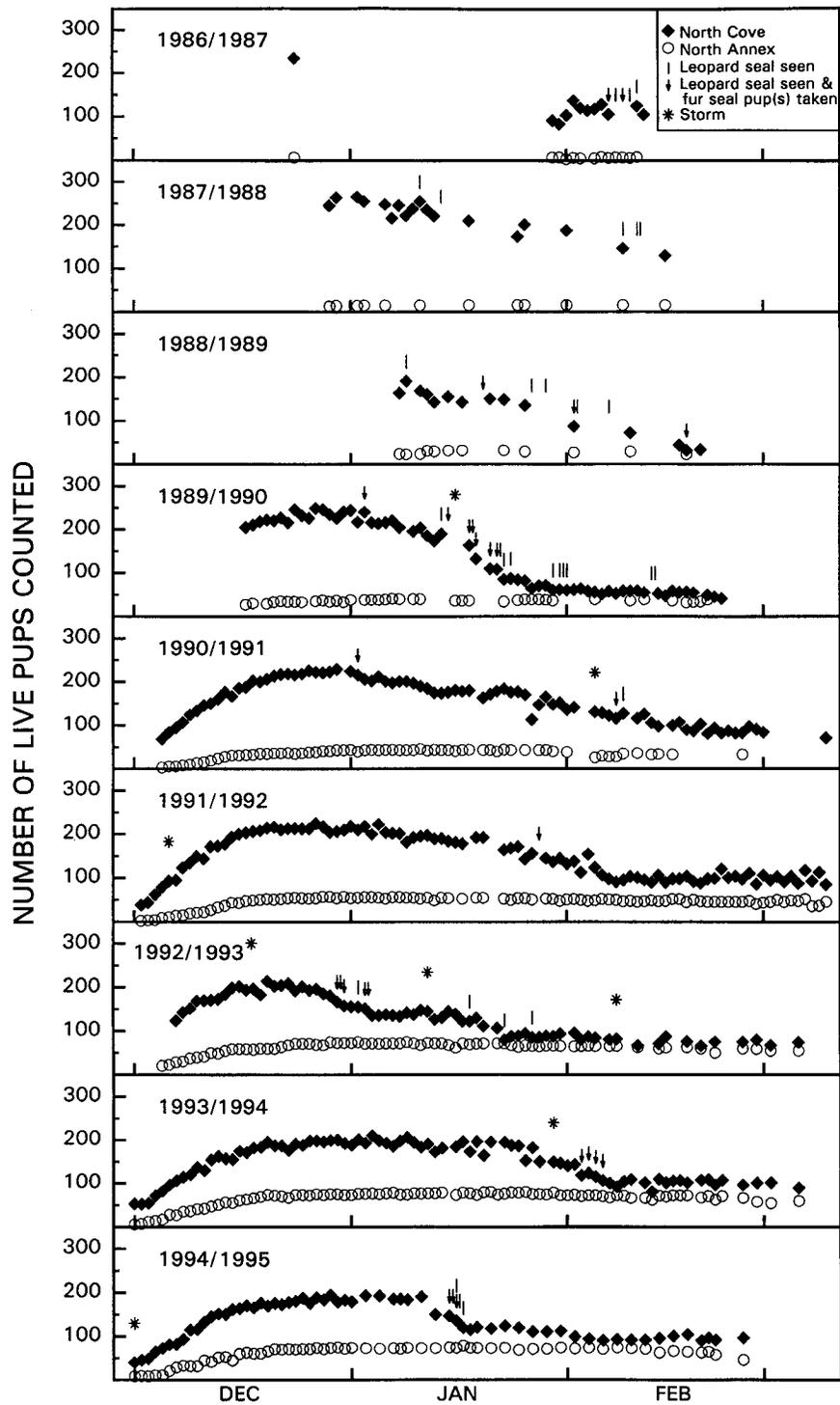


FIG. 2. Daily counts of Antarctic fur seal pups, sightings of leopard seals, and observations of leopard seals preying on fur seal pups at North Annex and North Cove colonies on Seal Island, Antarctica, during the austral summers of 1986/1987–1994/1995.

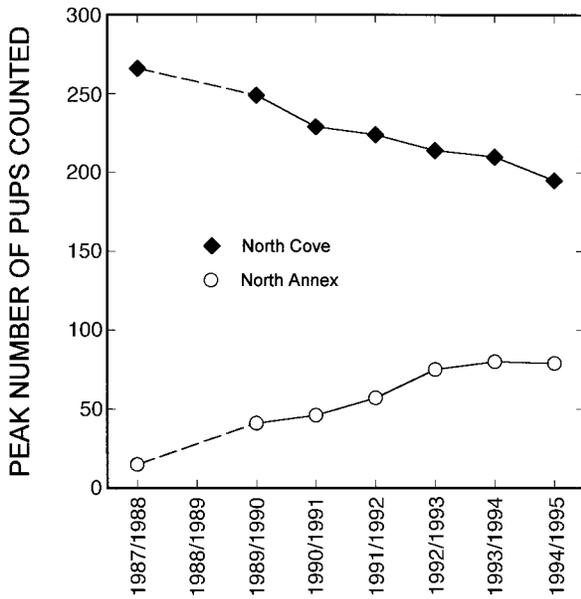


FIG. 3. Annual peak counts of Antarctic fur seal pups at North Annex and North Cove colonies on Seal Island, Antarctica, 1986/1987–1994/1995.

by leopard seals during the same period ranged from 32 to 38% of total births. Total pup mortality ranged from 51 to 66% (Table 2) and was probably even higher in 1989/1990 (~79%), given that the estimated number of pups taken by leopard seals in that year was twice the highest number seen in the other years (Table 2).

*Fur seal abundance and trends in the Elephant Island area*

The number of pups counted at the four main breeding sites in the Elephant Island area (Seal Island, Large Leap Island, Cape Lindsey, and Cape Valentine; Fig. 1) increased from 772 pups in 1986/1987 to 1010 pups in 1993/1994 (Table 3), indicating an annual growth rate of  $3.8 \pm 0.2\%$  (mean  $\pm 1$  SE,  $R^2 = 0.997$ ). In 1993/1994, two other small colonies were discovered in the northwestern islets of the Seal Islands archipelago, as well as one on the southern point of Cape Lindsey, Elephant Island (Table 3). There were at least 1096 fur seal pups born in the Elephant Island vicinity in 1993/1994 (Table 3), allowing for the fact that most of the colonies were counted after the expected peak of seasonal abundance. That number of pups would correspond to a total population of ~4500 fur seals if the age structure was similar to that at South Georgia in the early 1970s (Payne 1979).

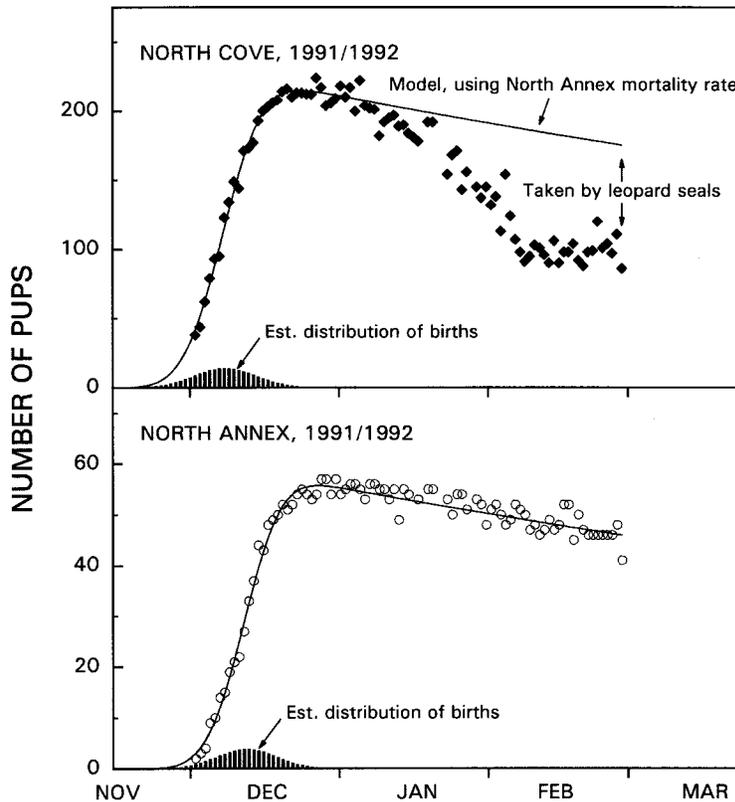


FIG. 4. A model of the chronology of births and pup mortality, fit to 1991/1992 Antarctic fur seal pup counts at North Annex and North Cove colonies on Seal Island. The  $\blacklozenge$ s and  $\circ$ s represent daily counts of live pups in the respective colonies.

TABLE 1. Estimates of the chronology of births, daily mortality rate, and total births of Antarctic fur seal pups at North Annex (NA) and North Cove (NC) colonies on Seal Island, Antarctica, 1990/1991–1994/1995. The annual peak counts of live pups and the number of dead pups observed prior to the peak count are shown for comparison.

Year	Colony	Model parameter estimates					Prop. variance explained ( $R^2$ )	
		Birthdate		Daily mortality rate	Total births	Peak live pup count		Dead pups
		Mean	SD (d)					
1990/1991	NA	14 Dec	8.7	0.0044	48	46	1	0.96
	NC	9 Dec	8.0	†	239	229	4	0.98‡
1991/1992	NA	12 Dec	6.1	0.0032	59	57	1	0.98
	NC	8 Dec	6.4	†	228	224	4	0.99‡
1992/1993	NA	10 Dec	10.3	0.0040	81	75	4	0.97
	NC	5 Dec	6.9	†	216	214	3	0.92‡
1993/1994	NA	10 Dec	8.0	0.0023	81	80	0	0.97
	NC	7 Dec	8.6	†	207	210	3	0.98‡
1994/1995	NA	11 Dec	8.1	0.0028	80	79	1	0.96
	NC	8 Dec	7.9	†	197	195	1	0.99‡
Average	NA	11 Dec	8.2	0.0033	70	67	1	...
	NC	7 Dec	7.6	†	217	214	3	...

† Daily mortality rate was held fixed at the same rate as at NA for that year.

‡ The model was fit only to counts obtained prior to the onset of predation at NC.

## DISCUSSION

### *Fur seal pup production and mortality at Seal Island*

*Assessment of model assumptions.*—The model for estimating breeding chronology and pup mortality was based upon three primary assumptions: (1) that birth dates are normally distributed, (2) that there is no leopard seal predation of fur seal pups at NA, and (3) that the daily rate of pup mortality from nonpredatory causes is the same at NA and NC and is constant throughout the breeding season.

Results from other studies of Antarctic fur seals support the first assumption. Although there is some variation attributable to seal age and food availability (Boyd et al. 1990, Duck 1990, Lunn and Boyd 1993a, b, Boyd 1996), individual females tend to give birth at the same time of the season each year (Boyd 1996). The duration of pregnancy in Antarctic fur seals appears to be normally distributed, and is highly corre-

lated with birth date (Boyd 1996). Thus, it seems reasonable to assume that birth dates are also normally distributed.

Our assumption that leopard seals did not prey on pups at NA was based on the fact that leopard seals were never observed there, despite the frequent sightings at nearby NC. Although observers spent more time at NC, it is very unlikely that leopard seals and predation were simply overlooked at NA. The colony was observed carefully during the daily pup count. Two to five observers had clear views of NA at various times throughout each day en route to and from research activities at NC. Because the lagoon and breeding beach at NA are small and close to the trail used by observers (0–40 m), a leopard seal at NA would have been conspicuous. We suppose that the shallowness of the surge channels connecting NA to the sea prevented leopard seals from gaining access to the lagoon.

That pup mortality from nonpredatory causes is

TABLE 2. Estimated numbers of Antarctic fur seal pups that died from predatory and non-predatory causes at the North Cove colony on Seal Island, 1989/1990–1994/1995. Numbers in parentheses are proportions of total births.

Year	Number of pups that died from nonpredatory causes	Number of pups taken by leopard seals	Total number of mortalities	Total births (estimated from model)
1989/1990†	25 (0.10)	165 (0.69)	190 (0.79)	...†
1990/1991	71 (0.30)	81 (0.34)	152 (0.64)	239
1991/1992	51 (0.22)	76 (0.33)	127 (0.56)	228
1992/1993	59 (0.27)	83 (0.38)	142 (0.66)	216
1993/1994	34 (0.16)	72 (0.35)	106 (0.51)	207
1994/1995	38 (0.19)	63 (0.32)	101 (0.51)	197

† Because counts began too late in the 1989/1990 breeding season (see Fig. 2), total births could not be estimated from the chronology model; an approximate estimate of 239 total births was obtained as the peak of the (smoothed) pup counts. The mortality estimates are therefore approximations, as well.

TABLE 3. Numbers of Antarctic fur seal pups (live plus dead) counted in the Elephant Island vicinity. The date of each count is given in parentheses. Blank entries designate that the colony was not counted.

Location	1986/ 1987†	1987/ 1988	1988/ 1989	1989/ 1990	1990/ 1991	1991/ 1992	1992/ 1993	1993/ 1994	1994/ 1995
Seal Island archipelago									
1) Seal Island‡	249§ (24 Dec)	281 (2 Jan)	214 (9 Jan)	293 (27 Dec)	283 (30 Dec)	297 (27 Dec)	300 (24 Dec)	302 (4 Jan)	286 (29 Dec)
2) Large Leap Island	275 (30 Jan)	279 (30 Jan)	237 (22 Jan)	254 (12 Jan)	228 (25 Jan)	258 (9 Feb)	314 (21 Jan)	306 (15 Jan)	319 (14 Jan)
3) Islets NW of Seal Island								68¶ (4 Feb)	94 (14 Jan)
Elephant Island									
4) Cape Lindsey, islets	203 (30 Jan)					241 (21 Feb#)		278 (2 Feb)	
5) Cape Lindsey, S point								18 (2 Feb)	
6) Cape Valentine	45 (23 Dec)					126 (19 Jan)		124 (4 Feb)	
Total of 1, 2, 4, and 6	772					922		1010	

† Data from Bengtson et al. 1990.

‡ Peak of daily combined counts at North Cove and North Annex, plus number of individual dead pups seen during daily surveys prior to the peak count. Also includes a small colony (7–15 pups), informally named Big Boote, not generally counted on same date as North Cove and North Annex.

§ Based on a count of 226 pups in a portion of the colony that typically contains about 91% of the total.

|| Islets informally named Transmitter Rock (60°58.42' S, 55°26.52' W) and Saddle Rock ("Cave Colony," 60°58.95' S, 55°24.88' W).

¶ Part of the colony, in a cave, was inaccessible and was estimated to contain 20 pups. A direct count in 1994/1995 revealed 42 pups in the cave.

# One islet off the northern tip of Cape Lindsey, with 14 pups, was counted on 19 January 1992.

equal at NA and NC also seems reasonable. Mortality rates of pups have been observed in other studies to vary with the density of pinnipeds in the breeding colony, and with various environmental characteristics of the colony (Coulson and Hickling 1964, Le Boeuf and Briggs 1977, Doidge et al. 1984, Harcourt 1992). Density and environmental conditions, however, probably do not lead to colony differences in pup mortality rates at Seal Island. Both NA and NC are low-density colonies (0.14 and 0.17 pups/m<sup>2</sup>, respectively; compare with the range of 0.15–1.5 pups/m<sup>2</sup> in colonies studied by Doidge et al. [1984]). The two colonies are close to one another, so that they experience the same weather and environmental conditions. Two aspects of our own results also support this assumption: First, the ratio of average number of dead pups (observed prior to the peak in live pups) to the peak live pup count (Table 2) was nearly identical at NA and NC. Second, if the true mortality rate at NC prior to the onset of predation had been much different than the assumed rate from NA, the estimates of number of births would have been inconsistent with the observed peak pup counts (because of the structural correlation between those parameters of the model), which was not the case (Table 1).

It may not be strictly true that the rate of pup mortality from nonpredatory causes is constant throughout the breeding season, but the resulting biases are likely to be small and to affect both colonies in the same way.

Storms and heavy waves on exposed beaches can separate pups from their mothers (Le Boeuf and Briggs 1977, Anderson et al. 1979, Boness et al. 1992), possibly imposing a random or episodic pattern on mortality rates. But, when storms with high waves occurred at NA and NC, pup counts generally returned to pre-storm levels within a few days (Fig. 2) as the colony regained its structure and pups returned from taking refuge above the margins of the colonies. Mortality is greatest in the first few days of life in Antarctic fur seals at South Georgia (Doidge et al. 1984) and in South African fur seals (*Arctocephalus pusillus* [De Villiers and Roux 1992]). Mortality is also higher for Antarctic fur seal pups born later in the season (Doidge et al. 1984), perhaps because younger females, which are generally smaller and in poorer condition than older females, give birth later in the pupping season (Lunn and Boyd 1993a). The potential biases from these factors are reduced by the spread in birth dates, which ensures a range of age and vulnerability to mortality in the pups alive on any particular date. It should be noted, however, that our estimates of daily mortality rate are the average values that are most consistent with the estimates of total births and breeding chronology in each year, and they may not be strictly applicable to any particular date or age of pups.

*Mortality of fur seal pups and the effect of predation by leopard seals.*—Our estimate of pup mortality from nonpredatory causes during the breeding season at Seal

Island (average of 22% at mean age of 75 d) was much higher than the 4.4% at 77 d of age reported for Antarctic fur seal pups at Heard Island by Shaughnessy and Goldsworthy (1990). They acknowledged, however, that theirs was an underestimate because an unknown number of dead pups that had been scavenged were not included. Cumulative mortality of Antarctic fur seal pups at Schlieper Bay, South Georgia—where seal density was nearly identical to densities at NA and NC—was 3–6% at the end of December (Doidge et al. 1984). For the same portion of the breeding season at Seal Island, our model gave estimates of 4.7–10%, somewhat higher than at Schlieper Bay. These differences may reflect genuinely higher mortality at Seal Island than at Heard Island and Schlieper Bay, but we suspect that the differences are due at least partially to incomplete recovery or detection of pup carcasses in the other two studies. Although it may not be practical for large pinniped colonies, we suggest that regular counts of live pups be used to check for consistency when pup mortality is estimated from sightings or recovery of dead pups.

The striking decline in pup numbers at NC each breeding season was likely due to leopard seal predation, as periods of rapid decline at NC corresponded to periods when leopard seals and predation on pups were observed (Fig. 2). Furthermore, leopard seals were not observed in NC after pup counts stabilized each year, even though they continued to be sighted elsewhere on the island. Estimates from the model suggest that an average of 34% of the NC pup cohort is lost to leopard seals prior to the end of February in a typical year, though leopard seals may take more of the cohort in some years, as indicated by our approximate estimate of 69% for 1989/1990 (Table 2). These values are high in comparison to other rates of predation on pinnipeds by marine mammal predators. Up to 8.3% of South American fur seal pups at a low-density beach were taken by southern sea lions (*Otaria byronia* [Harcourt 1992]). In the subantarctic Crozet Islands, killer whales (*Orcinus orca*) have been observed taking up to 25% of the southern elephant seal pups (*Mirounga leonina*) from one beach (Guinet and Jouventin 1990). Guinet et al. (1992) suggest that the southern elephant seal population has been declining over the past decades because of that predation.

*Fur seal trends at Seal Island.*—The declining trend in pup numbers at NC in recent years may reflect the fact that the high pup mortality at NC ( $\geq 51\%$  of pups at 75 d of age, Table 2) caused poor recruitment to that breeding colony. This can be demonstrated by adding our estimates of pup mortality to a life table for female fur seals of age  $\geq 2$  yr at Bird Island, South Georgia (Boyd et al. 1995) and calculating the expected population growth rates (given reasonable assumptions about survival from the breeding season to age 2 yr). Using our estimate of 22% pup mortality from non-predatory causes, a slightly positive population growth

rate of  $\sim 0.5\%$  would be expected. Adding our estimate of 34% pup mortality from leopard seal predation at NC would produce a population decline of 6%/yr, not greatly different from the observed decline of 4.2%/yr at NC.

Because research activities were more frequent at NC than at NA, we considered whether human disturbance could have caused mortality or movements that influenced the NC decline (Mattlin 1978, Lunn and Boyd 1991). Pups were weighed and marked or tagged at 14-d intervals beginning in late December at NC and in mid-January at NA, but we observed no injury or mortality that could be attributed to this handling. At NC, 222 perinatal fur seals were handled for attaching instruments (Walker and Boveng 1995), and the seals' behavior was monitored after instrumentation; 93% stayed near the area in which they were captured at NC. Thus, even though NC was disturbed more frequently than NA, we observed no disturbance-related pup mortality or shifts in seals' preferences for breeding sites that would explain the population decline at NC. Predation by leopard seals, with a consequent drop in recruitment, remains the most likely cause of the decline.

We do not know when leopard seal predation and the decline in fur seal births began at NC, but our results indicate that they were already underway when we began this study (Figs. 2 and 3). Hunt (1973) observed 16 fur seal pups on 13–14 December 1970 at Seal Island, all in one colony that presumably was NC. Assuming that he counted all the live pups and that half the pups had yet to be born,  $\sim 32$  pups would have been born that year. The colony must have grown substantially before beginning the present decline, perhaps in the early 1980s. (A forward projection from 1970/1971 with a growth rate of 25%/yr as we observed at NA, and a backward projection from the 4.2% decline in our observed counts from NC, would intersect at a value of 380 pups in 1981/1982.)

We have very few data from which to estimate the frequency of leopard seal predation at other fur seal colonies in the Elephant Island vicinity. However, on the two occasions when we were able to count pups twice in one season, the second count was lower by more than would be expected in the absence of predation: In 1989/1990, a second count of 132 fur seal pups at the Large Leap colony on 27 February indicated that daily pup mortality there had been  $\sim 1.4\%$  since the earlier count on 12 January (Table 3), over four times the average mortality rate at NA on Seal Island. At Cape Lindsey, counts obtained on 19 January and 21 February 1992 indicated a daily decline of  $\sim 0.5\%$ , slightly greater than our highest estimate for NA. The actual mortality was likely  $>0.5\%$ , however, because the first count was obtained by observations at a greater distance than the second count and is likely to have underestimated the initial number of pups. The colonies at Large Leap Island and Cape Lindsey are adjacent to several tidal lagoons in which fur seal pups develop

their swimming abilities; these lagoons appeared to be as accessible to leopard seals as the lagoon in which leopard seals hunt fur seal pups at NC on Seal Island (L. M. Hiruki et al., *unpublished manuscript*). It seems plausible, therefore, that leopard seals may cause substantial pup mortality at these colonies, as well. These possibilities, and our results describing the distribution of fur seal birth dates and onset of leopard seal predation at Seal Island, indicate that accurate monitoring of future population trends would be facilitated by pup counts obtained on or about 1 January, just after births are complete but before significant predation occurs.

#### *Fur seal trends at the South Shetland Islands and South Georgia*

The overall fur seal population of the South Shetland Islands has been increasing since counts began in the mid-1960s (Oliva et al. 1987, Aguayo and Torres 1993). In the Elephant Island area, comprising Elephant Island and the Seal Islands archipelago (Fig. 1), fur seals increased from four breeding colonies with 13 pups observed in February of 1966 (Aguayo and Torres 1967, Aguayo 1978) to a population producing at least 1096 pups in 1993/1994 (Table 3). The 3.8% annual rate of increase in pup numbers at the four locations counted in 1986/1987, 1991/1992, and 1993/1994 (Table 3) was much lower than the 11% annual increase in pup counts from 1986/1987 and 1991/1992 at Cape Shirreff (Livingston Island) and nearby San Telmo Island, the largest fur seal colonies in the South Shetlands (5313 pups [Aguayo and Torres 1993]). Clearly, the portion of the population in the Elephant Island vicinity has been growing much more slowly than that of Livingston Island.

Antarctic fur seal colonies at South Georgia re-established themselves more quickly following exploitation, which ended in ~1907 (Bonner 1968). There, the species' recovery probably began from a remnant group of seals at Bird and Main Islands off the northwest end of South Georgia (Bonner 1968). Pups were first seen there in the 1930s (Mackintosh 1967) and Bonner and Laws (1964) estimated that by 1956 there were 13 000 fur seals there. The South Georgia fur seal population was estimated to be  $>1.5 \times 10^6$  individuals in 1990/1991 (Boyd 1993). The annual rate of increase in pup production was as high as 13.5% (Wickens and York 1997) or 16.8% (Payne 1977) in the 1960s and early 1970s, dropping to 9.8% between 1976/1977 and 1990/1991 as densities reached saturation at the sites that were colonized first (Boyd 1993). In comparison, the South Shetland Island population has grown only to ~30 000 seals, even though it has probably been free from harvesting for 20 yr longer than the South Georgia population (Bonner 1968). Growth rates of the main colonies in the South Shetlands have not exceeded 11%/yr even though densities of the breeding colonies are much lower than most at South Georgia (J. L. Bengtson and P. L. Boveng, *personal observation*).

#### *Top-down control of fur seal populations*

Although we have shown that leopard seals can reverse the recovery of a local population of fur seals such as the NC colony at Seal Island, it remains uncertain whether any broader population of fur seals is limited or regulated by predators. In the remainder of this paper, we discuss circumstantial evidence that is consistent with a significant role of leopard seals in the dynamics of the fur seal population in the South Shetland Islands. We then discuss the species interactions between leopard and fur seals, and the similarity of certain aspects of those interactions to other vertebrate predator-prey systems, especially with regard to whether density-dependent regulation of fur seals by leopard seals is plausible. Finally, we speculate briefly about why predation by leopard seals has apparently increased in importance, at least at NC on Seal Island in recent years.

*Evidence for predation-limited growth in the South Shetland Islands.*—The long-term rates of recovery from commercial extinction are consistent with a hypothesis that leopard seals have had much less impact on the fur seal population of South Georgia than on the population of the South Shetlands. Recovery at South Georgia from commercial extinction in 1907 (assuming arbitrarily that 100 fur seals remained) to a population of ~28 000 in 1958 (Payne 1977, 1979) would have required an average annual increase of ~12%, a rather high, sustained growth rate (Wickens and York 1997). In contrast, fur seal recovery in the South Shetlands from commercial extinction in 1888 (Bonner 1968) to a population of ~30 000 in 1995 represents only ~5% annual growth.

Recent observations of leopard seal abundance and growth rates of local fur seal populations are consistent with the long-term trends. McCann and Doidge (1987) remarked that predation by leopard seals (and killer whales) seemed insignificant in regulating the fur seal population at South Georgia; leopard seals are generally absent during the summer fur seal breeding season, though they do take juvenile fur seals there in winter (Bonner 1958, Walker et al. 1998). Fur seal researchers at Livingston Island observed a maximum of two leopard seals each austral summer from 1990/1991 to 1994/1995 (D. Torres, *personal communication*). No predation on fur seal pups was observed there until 1995/1996, when eight leopard seals were sighted. As we documented in the present study, leopard seals have preyed heavily on fur seal pups at Seal Island and perhaps other colonies in the Elephant Island area at least since 1986/1987 when observations began. Thus, abundance of leopard seals and rate of predation on fur seals seem to have been low at South Georgia (where the fur seal population growth rate has been the highest) and higher in the South Shetland Islands, especially in the Elephant Island area, where growth of fur seal populations has been slowest.

The relative abundance of leopard seals in summer at South Georgia and the South Shetland Islands may be a function of proximity to sea ice (Bonner and Laws 1964); most leopard seals are found in the pack-ice zone (Gilbert and Erickson 1977). This is consistent with the absence of leopard seals in the summer at South Georgia, where the nearest sea ice in January is typically 700–900 km south, and the common presence of leopard seals in the summer at the South Shetland Islands (Aguayo 1970, Rakusa-Suszczewski and Sierakowski 1993), where the ice is usually within 200 km in January.

Another factor, in addition to local abundance of leopard seals, that could lead to differences in predation rates among fur seal colonies at South Georgia, Livingston Island, and the Elephant Island area is the topography of fur seal colonies and surroundings. At South Georgia, fur seals prefer breeding sites that are backed by vegetated slopes (Boyd 1993). Unattended pups commonly roam or rest in the tussock grass on the slopes and join their mothers there to nurse. These pups may spend less time in the water—exposed to leopard seals—than pups in the Elephant Island area where colonies are backed by steep, rocky slopes. The terrain surrounding colonies at Livingston Island (Cape Shirreff) is gently sloping, open, and accessible to pups but has no tussock grass for cover; pups roam inland, but may spend less time there than pups at South Georgia because they would be more exposed to harassment by giant petrels (*Macronectes giganteus*), skuas (*Catharacta* spp.), and subadult male fur seals. Whether these differences in topography and cover actually correspond to differences in fur seal pup behavior could be tested by relatively simple measures of pup activity budgets (i.e., proportion of time spent in the water) at the three locations.

In other research associated with this study, (e.g., Bengtson et al. 1994) we monitored foraging and reproductive performance of Antarctic fur seals at Seal Island. During the 9 yr of research, we observed no evidence of extreme food limitation in fur seals such as occurred in 1977/1978, 1983/1984, 1990/1991, and 1993/1994 when krill were scarce around South Georgia (Croxall et al. 1988, Brierley and Watkins 1996). Preliminary analyses of measures such as growth rates of pups and durations of maternal foraging trips (J. L. Bengtson, *unpublished data*) indicate that food availability to fur seals at Seal Island is typically comparable to or greater than that at South Georgia (Lunn et al. 1993, Boyd et al. 1994). Thus, bottom-up forces may be less strong or exert themselves less frequently in the Elephant Island vicinity than at South Georgia.

Although these observations do not provide conclusive evidence that predation is a major force limiting fur seal population growth and recovery in the South Shetland Islands, we believe that top-down limitation should be given a greater focus in working hypotheses that guide further research on this population.

*Relevance to other vertebrate predator-prey systems.*—Compared with the well-studied terrestrial systems of vertebrate predators and prey in the northern hemisphere, such as wolves and moose (Messier 1994), lynx and hares (Sinclair et al. 1993), and mustelids and rodents (Hanski and Henttonen 1996), very little is known of the quantitative nature of the relationship between leopard seals and fur seals. However, it is possible to make qualitative inferences about the primary features of this relationship, and about whether leopard seals are capable of regulating fur seal populations, by considering the historical dynamics of the fur seals' recovery from exploitation.

As we discussed earlier, the fur seal population of the South Shetland Islands has recovered rather slowly from overharvesting. Nevertheless, this population did grow and the growth does not appear to be decelerating (Bengtson et al. 1990, Aguayo and Torres 1993), even in the Elephant Island area (Table 3). Long-term, steady growth rules out certain conceptual models for the predator-prey relationship between leopard seals and fur seals. For example, a scenario like that depicted in Fig. 5a is unlikely to reflect the conditions of the recovery in the South Shetlands. In that scenario, strongly density-dependent predation mortality would be capable of maintaining the fur seal population in a "predator pit" at low densities (e.g., Pech et al. 1995). Decelerating growth would be expected as the recovering population increased toward a low equilibrium regulated by density-dependent predation ( $E_p$ ).

Messier (1994) suggested that strong density-dependent predation of moose by wolves occurred because moose are spatially predictable, available year-round, and alternative prey species are occasionally or seasonally rare. Fur seals share some of these traits, but not others. They are spatially predictable for ~4 mo during the breeding and pup-rearing season. However, because leopard seals prey mainly on young-of-the-year fur seals, which tend to disperse after weaning, fur seals may not be a reliable year-round food source. Leopard seals have many alternatives to fur seals as prey, including other seal species, seabirds, fish, cephalopods, and krill (Siniff and Stone 1985). Therefore, the rate of predation on fur seals by leopard seals may be less strongly dependent on prey density than the rate of predation on moose by wolves. Because relatively few individual leopard seals may be responsible for most of the predation of fur seal pups in the South Shetland Islands (Rakusa-Suszczewski and Sierakowski 1993; L. M. Hiruki et al., *unpublished manuscript*) the predation rate may even be inversely dependent on density; the per capita rate of predation may decline with increasing fur seal density (Pech et al. 1995). Fig. 5b depicts an example of such a scenario; leopard seal predators consume a substantial fraction of the net production, allowing fur seals to slowly increase to a level at which they are essentially limited by some resource such as food or space (equilibrium density  $E_p$ ). The

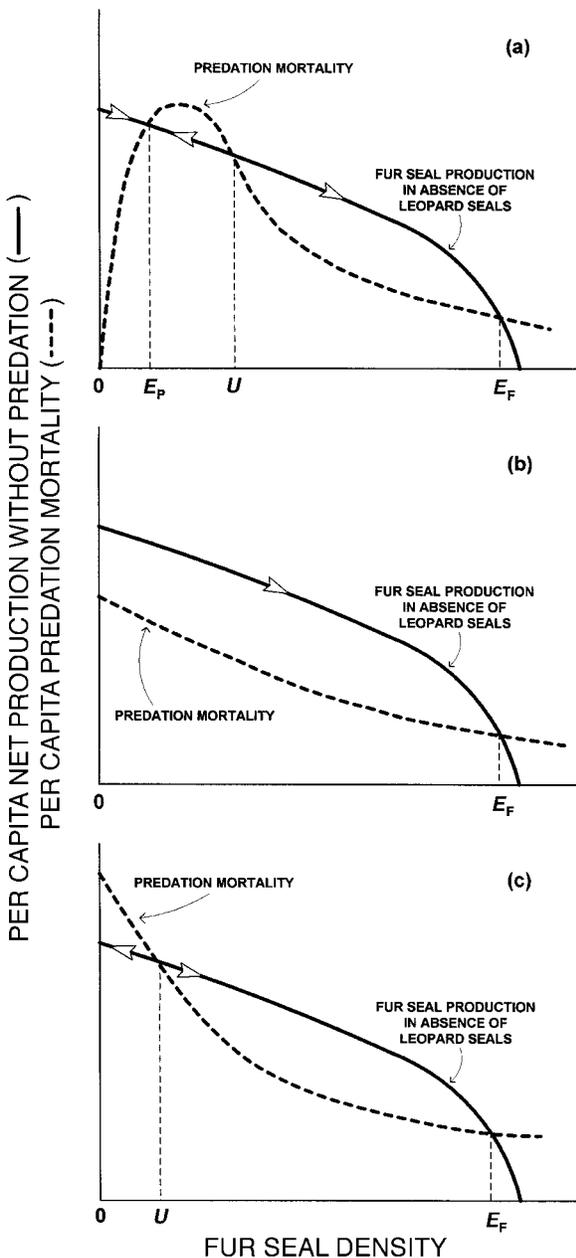


FIG. 5. Conceptual models of the predator-prey relationship between leopard seals and Antarctic fur seals. Net production of fur seals in the absence of predation by leopard seals is assumed to be density dependent with limitation by space and/or food at high densities. In part (a), predation mortality is density-dependent at low densities of fur seals and inversely density-dependent at moderate to high densities, producing a stable, low-density equilibrium ( $E_p$ , "predator pit"), an unstable equilibrium ( $U$ ), and an equilibrium at high density ( $E_F$ ) that is limited mostly by resources. In (b), predation mortality is inversely dependent on density, with just one resource-limited equilibrium. In (c), the predation rate is higher than in (b), producing a destabilizing condition at low densities (i.e., near  $U$ ).

growth rate of the fur seals would be modest and constant or slightly increasing (accelerating) at low to moderate densities.

The sizes and densities of the fur seal populations prior to commercial depletion are uncertain. By one account, however, 320 000 fur seal skins were taken from the South Shetland Islands in 1821–1822, the peak years of the short-lived harvest (Weddell 1825). If that number represented the entire population prior to the harvest, the overall density of the present population is only ~10% of what the habitat was once able to support. Therefore, it may be difficult to predict the response of predation rate to moderate or high fur seal densities. For now, we can only conclude that rates of predation by leopard seals on the fur seal population of the South Shetland Islands have remained, on average, below the rate of fur seal production and that leopard seals do not seem to be capable of regulating that fur seal population at low density.

These conclusions highlight one important difference between the leopard seal–fur seal system and the better-understood northern terrestrial systems: A broad-scale perturbation, or "prey removal experiment," was inadvertently conducted by harvesting fur seals to commercial extinction. The prolonged recovery during the past several decades allows qualitative inferences to be made about some of the main features of the predator–prey relationship, something that is not often possible when the prey (and/or predator) species undergoes irregular cycles or irruptions, as is common in the northern hemisphere systems.

What can be said about the NC fur seal colony at Seal Island, the one case in which leopard seals have clearly reversed the fur seals' recovery? The steady decline in fur seal births over a period of  $\geq 7$  yr at NC (Fig. 3) may indicate a destabilizing effect of predation on fur seal density. An example of a simple model with unstable dynamics at low fur seal density is shown in Fig. 5c. If the fur seal population was perturbed to a density below the unstable equilibrium  $U$ , or if predation mortality increased so that  $U$  became greater than the fur seal density, an accelerating decline to extinction would ensue. The same conditions could also prevent the establishment of a breeding colony that had previously gone extinct, as may be the case at sites where South African fur seals haul out but fail to establish breeding colonies because of predation of fur seal pups by jackals (*Canis mesomelas* [Oosthuizen et al. 1997]). Although the model of Fig. 5c is one possible description of the recent dynamics of the fur seal population at NC, it does not provide an explanation of why predation by leopard seals seems to have become more important in the past two decades.

*Temporal context of increased predation by leopard seals.*—The models in Fig. 5 are, of course, overly simplistic in many respects. One important respect is the lack of stochasticity in the production and predation curves. Recent studies of variability in the Antarctic

marine environment indicate that there is no reason to expect equilibrium conditions in the dynamics of the krill-based food web of marine vertebrates. For example, leopard seal abundance at several Antarctic islands varies dramatically from year to year, possibly even in a cyclic fashion (Rounsevell and Eberhard 1980, Rakusa-Suszczewski and Sierakowski 1993, Walker et al. 1998). This variation alone could cause shifts in the predation curve so that some years reflect the conditions of Fig. 5c, while in other years predation is lower (as in Fig. 5b) or even absent. But there are many more examples of broad-scale variation in the Antarctic marine environment: Populations of crabeater seals (*Lobodon carcinophagus*), another species preyed upon by leopard seals, also display quasi-cyclic variation (Testa et al. 1991, Boveng and Bengtson 1997). Numbers of male fur seals visiting South Orkney and South Shetland Islands have increased dramatically (faster than overall abundance at South Georgia and South Shetlands) in the past two decades (Hodgson and Johnston 1997, Smith 1997). A "circumpolar wave" of coupled variation in sea-ice extent, sea surface temperature, atmospheric pressure, and wind stress causes environmental conditions to cycle with a period of 4–5 yr (White and Peterson 1996). Sea-ice extent declined rapidly between the 1950s and the 1970s, but it has remained roughly constant since then (de la Mare 1997). Because of the great potential for complex interactions between the processes reflected in these examples, we are reluctant to speculate in more detail about why predation by leopard seals would rather suddenly reverse the recovery of a fur seal colony such as NC.

We suggest that future research on the demography of Antarctic fur seals in the South Shetland Islands should include efforts to monitor the importance of predation by leopard seals at the main fur seal colonies. Whether the fur seal population of the South Shetland Islands ultimately becomes limited by resources or regulated by predation may depend upon the number and sizes of colonies that are exposed to predation, such as NC, relative to the number and sizes of colonies that are refuges from predation (Sih 1987, Taylor and Pkins 1991), such as NA.

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#### LITERATURE CITED

- Aguayo L., A. 1970. Census of pinnipedia in the South Shetland Islands. Pages 395–397 in M. W. Holdgate, editor. Antarctic ecology. Academic Press, London, UK.

- . 1978. The present status of the Antarctic fur seal *Arctocephalus gazella* at South Shetland Islands. Polar Record **19**:167–176.
- Aguayo L., A., and D. Torres N. 1967. Observaciones sobre mamíferos marinos durante la vigésima comision antartica chilena. Primer censo de pinipedios en las Islas Shetland del Sur. Revista Biología Marina **13**:1–53.
- Aguayo L., A., and D. Torres N. 1993. Census analysis of *Arctocephalus gazella* on the Site of Special Scientific Interest No. 32, Livingston Island, Antarctica. Serie Científica Instituto Antártico Chileno **43**:87–91.
- Ainley, D. G., W. J. Sydeman, and J. Norton. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. Marine Ecology Progress Series **118**:69–79.
- Anderson, S. S., J. R. Baker, J. H. Prime, and A. Baird. 1979. Mortality in grey seal pups: incidence and causes. Journal of Zoology, London **189**:407–417.
- Baker, J. R., and D. W. Doidge. 1984. Pathology of the Antarctic fur seal (*Arctocephalus gazella*) in South Georgia. British Veterinary Journal **140**:210–219.
- Bengtson, J. L., P. L. Boveng, L. M. Hiruki, J. K. Jansen, W. R. Meyer, M. K. Schwartz, and B. G. Walker. 1994. Antarctic Marine Living Resources program: pinniped and seabird studies at Seal Island, South Shetland Islands, during the 1993–1994 austral summer. Antarctic Journal of the United States **29**(5):200–201.
- Bengtson, J. L., L. M. Ferm, T. J. Härkönen, and B. S. Stewart. 1990. Abundance of Antarctic fur seals in the South Shetland Islands, Antarctica, during the 1986/87 austral summer. Pages 265–270 in K. R. Kerry and G. Hempel, editors. Antarctic ecosystems, ecological change and conservation. Springer-Verlag, Berlin, Germany.
- Boness, D. J., D. Bowen, S. J. Iverson, and O. T. Oftedal. 1992. Influence of storms and maternal size on mother-pup separations and fostering in the harbor seal, *Phoca vitulina*. Canadian Journal of Zoology **70**:1640–1644.
- Bonner, W. N. 1958. Notes on the southern fur seal in South Georgia. Proceedings of the Zoological Society of London **130**:241–252.
- . 1968. The fur seal of South Georgia. British Antarctic Survey Scientific Reports **56**:1–81.
- Bonner, W. N., and R. M. Laws. 1964. Seals and sealing. Pages 163–190 in R. Priestley, R. J. Adie, and G. de Q. Robin, editors. Antarctic research. Butterworth, London, United Kingdom.
- Boveng, P. L., and J. L. Bengtson. 1997. Crabeater seal cohort variation: demographic signal or statistical noise? Pages 241–247 in B. Battaglia, J. Valencia, and D. W. H. Walton, editors. Antarctic communities. Species, structure and survival. Cambridge University Press, Cambridge, UK.
- Boyd, I. L. 1993. Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. Antarctic Science **5**:17–24.
- . 1996. Individual variation in the duration of pregnancy and birth date in Antarctic fur seals: the role of environment, age, and sex of fetus. Journal of Mammalogy **77**:124–133.
- Boyd, I. L., J. P. Y. Arnould, T. Barton, and J. P. Croxall. 1994. Foraging behavior of the Antarctic fur seal during periods of contrasting prey abundance. Journal of Animal Ecology **63**:703–713.
- Boyd, I. L., J. P. Croxall, N. J. Lunn, and K. Reid. 1995. Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. Journal of Animal Ecology **64**:505–518.
- Boyd, I. L., N. J. Lunn, P. Rothery, and J. P. Croxall. 1990. Age distribution of breeding female Antarctic fur seals in relation to changes in population growth rate. Canadian Journal of Zoology **68**:2209–2213.

- Brierley, A. S., and J. L. Watkins. 1996. Acoustic targets at South Georgia and the South Orkney Islands during a season of krill scarcity. *Marine Ecology Progress Series* **138**: 51–61.
- Cleveland, W. S. 1979. Robust locally weighted regression and smoothing scatterplots. *Journal of the American Statistical Association* **74**:829–836.
- Coulson, J. C., and G. Hickling. 1964. The breeding biology of the grey seal, *Halichoerus grypus* (Fab.), on the Farne Islands, Northumberland. *Journal of Animal Ecology* **33**: 485–512.
- Croxall, J. P., and M. N. Pilcher. 1984. Characteristics of krill *Euphausia superba* eaten by Antarctic fur seals *Arctocephalus gazella* at South Georgia. *British Antarctic Survey Bulletin* **63**:117–125.
- Croxall, J. P., T. S. McCann, P. A. Prince, and C. B. Sear. 1988. Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976–1987: implications for Southern Ocean monitoring studies. Pages 261–285 in D. Sahrhage, editor. *Antarctic ocean and resources variability*. Springer-Verlag, Berlin, Germany.
- de la Mare, W. K. 1997. Abrupt mid-twentieth-century decline in Antarctic sea-ice extent from whaling records. *Nature* **389**:57–60.
- De Villiers, D. J., and J.-P. Roux. 1992. Mortality of newborn pups of the South African fur seal *Arctocephalus pusillus pusillus* in Namibia. *South African Journal of Marine Science* **12**:881–889.
- Doidge, D. W., J. P. Croxall, and J. R. Baker. 1984. Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. *Journal of Zoology, London* **202**:449–460.
- Duck, C. D. 1990. Annual variation in the timing of reproduction in Antarctic fur seals, *Arctocephalus gazella*, at Bird Island, South Georgia. *Journal of Zoology, London* **222**:103–116.
- Gilbert, J. R., and A. W. Erickson. 1977. Distribution and abundance of seals in the pack ice of the Pacific sector of the Southern Ocean. Pages 703–740 in G. A. Llano, editor. *Adaptations within antarctic ecosystems*. Proceedings of the third Scientific Committee on Antarctic Research symposium on Antarctic Biology. Smithsonian Institution, Washington, D.C., USA.
- Green, K., H. R. Burton, and R. Williams. 1989. The diet of Antarctic fur seals *Arctocephalus gazella* (Peters) during the breeding season at Heard Island. *Antarctic Science* **1**: 317–324.
- Green, K., R. Williams, and H. R. Burton. 1991. The diet of Antarctic fur seals during the late autumn and early winter around Heard Island. *Antarctic Science* **3**:359–361.
- Guinet, C., and P. Jouventin. 1990. La vie sociale de la “baléine Tueuse”. *Recherche* **21**:508–510.
- Guinet, C., P. Jouventin, and H. Weimerskirch. 1992. Population changes, movements of southern elephant seals on Crozet and Kerguelen Archipelagos in the last decades. *Polar Biology* **12**:349–356.
- Hanski, I., and H. Henttonen. 1996. Predation on competing rodent species: a simple explanation of complex patterns. *Journal of Animal Ecology* **65**:220–232.
- Harcourt, R. 1992. Factors affecting early mortality in the South American fur seal (*Arctocephalus australis*) in Peru: density-related effects and predation. *Journal of Zoology, London* **226**:259–270.
- Hodgson, D. A., and N. M. Johnston. 1997. Inferring seal populations from lake sediments. *Nature* **387**:30–31.
- Hunt, J. F. 1973. Observations on the seals of Elephant Island, South Shetland Islands, 1970–71. *British Antarctic Survey Bulletin* **36**:99–104.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**: 724–732.
- Kovacs, K. M., D. M. Lavigne, and R. E. A. Stewart. 1985. Early postnatal mortality in northwest Atlantic harp seals (*Phoca groenlandica*). *Journal of Mammalogy* **66**:556–558.
- Le Boeuf, B. J., and K. T. Briggs. 1977. The cost of living in a seal harem. *Mammalia* **41**:167–195.
- Lunn, N. J., and I. L. Boyd. 1991. Popping-site fidelity of Antarctic fur seals at Bird Island, South Georgia. *Journal of Mammalogy* **72**:202–206.
- Lunn, N. J., and I. L. Boyd. 1993a. Effects of maternal age and condition on parturition and the perinatal period of Antarctic fur seals. *Journal of Zoology, London* **229**:55–67.
- Lunn, N. J., and I. L. Boyd. 1993b. Influence of maternal characteristics and environmental variation on reproduction in Antarctic fur seals. Pages 115–129 in I. L. Boyd, editor. *Marine mammals: advances in behavioural and population biology*. Clarendon, Oxford, UK.
- Lunn, N. J., I. L. Boyd, T. Barton, and J. P. Croxall. 1993. Factors affecting the growth rate and mass at weaning of Antarctic fur seals at Bird Island, South Georgia. *Journal of Mammalogy* **74**:908–919.
- Mackintosh, N. A. 1967. Estimates of local seal populations in the Antarctic, 1930/37. *Norsk Hvalfangst-Tidende* **3**:57–64.
- Mattlin, R. H. 1978. Pup mortality of the New Zealand fur seal (*Arctocephalus forsteri* Lesson). *New Zealand Journal of Ecology* **1**:138–144.
- McCann, T. S. and D. W. Doidge. 1987. Antarctic fur seal, *Arctocephalus gazella*. Pages 5–8 in J. P. Croxall and R. L. Gentry, editors. *Status, biology, and ecology of fur seals*. National Oceanic and Atmospheric Administration Technical Report National Marine Fisheries Service 51. United States Department of Commerce, Washington, D.C., USA.
- Messier, F. 1994. Ungulate population models with predation: a case study with the North American moose. *Ecology* **75**:478–488.
- Monaghan, P. 1996. Relevance of the behaviour of seabirds to the conservation of marine environments. *Oikos* **77**:227–237.
- O’Gorman, F. A. 1961. Fur seals breeding in the Falkland Islands dependencies. *Nature* **192**:914–916.
- Oliva, D., R. Duran, M. Gajardo, and D. Torres. 1987. Numerical changes in the population of the Antarctic fur seals *Arctocephalus gazella* at two localities of the South Shetland Islands. *Serie Científica Instituto Antártico Chileno* **36**:135–144.
- Oosthuizen, W. H., M. A. Meyer, J. H. M. David, N. M. Summers, P. G. H. Kotze, S. W. Swanson, and P. D. Shaughnessy. 1997. Variation in jackal numbers at the Van Reenen Bay seal colony with comment on likely importance of jackals as predators. *South African Journal of Wildlife Research* **27**:26–29.
- Payne, M. R. 1977. Growth of a fur seal population. *Philosophical Transactions of the Royal Society of London B* **279**:67–79.
- . 1979. Growth in the Antarctic fur seal *Arctocephalus gazella*. 1979. *Journal of Zoology, London* **187**:1–20.
- Pech, R. P., A. R. E. Sinclair, and A. E. Newsome. 1995. Predation models for primary and secondary prey species. *Wildlife Research* **22**:55–64.
- Press, W. H., S. A. Teukolsky, W. T. Vetterling, and B. P. Flannery. 1992. *Numerical recipes*, second edition. Cambridge University Press, New York, New York, USA.
- Rakusa-Suszczewski, S., and K. Sierakowski. 1993. Pinnipeds in Admiralty Bay, King George Island, South Shetlands (1988–1992). *Polish Polar Research* **14**:441–454.
- Reid, K. 1995. The diet of Antarctic fur seals (*Arctocephalus*

- gazella* Peters 1875) during winter at South Georgia. *Antarctic Science* **7**:241–249.
- Reid, K., and J. P. Y. Arnould. 1996. The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biology* **16**:105–114.
- Rounsevell, D., and I. Eberhard. 1980. Leopard seals, *Hydrurga leptonyx* (Pinnipedia), at Macquarie Island from 1949 to 1979. *Australian Wildlife Research* **7**:403–415.
- Shaughnessy, P. D., and S. D. Goldworthy. 1990. Population size and breeding season of the Antarctic fur seal *Arctocephalus gazella* at Heard Island—1987/88. *Marine Mammal Science* **6**:292–304.
- Sih, A. 1987. Prey refuges and predator–prey stability. *Theoretical Population Biology* **31**:1–12.
- Sinclair, A. R. E., J. M. Gosline, G. Holdsworth, C. J. Krebs, S. Boutin, J. N. M. Smith, R. Boonstra, and M. Dale. 1993. Can the solar cycle and climate synchronize the snowshoe hare cycle in Canada? Evidence from tree rings and ice cores. *American Naturalist* **141**:173–198.
- Siniff, D. B., and S. Stone. 1985. The role of the leopard seal in the tropho-dynamics of the Antarctic marine ecosystem. Pages 555–560 in W. R. Siegfried, P. R. Condy, and R. M. Laws, editors. *Antarctic nutrient cycles and food webs*. Springer-Verlag, Berlin, Germany.
- Smith, R. I. L. 1997. Impact of an increasing fur seal population on Antarctic plant communities: resilience and recovery. Pages 432–436 in B. Battaglia, J. Valencia, and D. W. H. Walton, editors. *Antarctic communities*. Species, structure and survival. Cambridge University Press, Cambridge, UK.
- Taylor, R. J., and P. J. Pekins. 1991. Territory boundary avoidance as a stabilizing factor in wolf–deer interactions. *Theoretical Population Biology* **39**:115–128.
- Testa, J. W., G. Oehlert, D. G. Ainley, J. L. Bengtson, D. B. Siniff, R. M. Laws, and D. Rounsevell. 1991. Temporal variability in Antarctic marine ecosystems: periodic fluctuations in the phocid seals. *Canadian Journal of Fisheries and Aquatic Sciences* **48**:631–639.
- Trillmich, F., and K. A. Ono, editors. 1991. *Pinnipeds and El Niño: responses to environmental stress*. Springer-Verlag, Berlin, Germany.
- Walker, B. G., and P. L. Boveng. 1995. Effects of time–depth recorders on maternal foraging and attendance behavior of Antarctic fur seals (*Arctocephalus gazella*). *Canadian Journal of Zoology* **73**:1538–1544.
- Walker, T. R., I. L. Boyd, D. J. McCafferty, N. Huin, R. I. Taylor, and K. Reid. 1998. Seasonal occurrence and diet of leopard seals (*Hydrurga leptonyx*) at Bird Island, South Georgia. *Antarctic Science* **10**:75–81.
- Weddell, J. 1825. *A voyage towards the South Pole, performed in the years 1822–24*. Longman, Hurst, Rees, Orme, Brown, and Green, London, UK.
- White, W. B., and R. G. Peterson. 1996. An Antarctic circumpolar wave in surface pressure, wind, temperature and sea-ice extent. *Nature* **380**:699–702.
- Wickens, P., and A. E. York. 1997. Comparative population dynamics of fur seals. *Marine Mammal Science* **13**:241–292.