Long-term evaluation of pup growth and preweaning survival rates in subantarctic fur seals, *Arctocephalus tropicalis*, on Amsterdam Island

Magaly Chambellant, Gwénaël Beauplet, Christophe Guinet, and Jean-Yves Georges

Abstract: This study is the first to investigate pup preweaning growth and survival rates over seven consecutive breeding seasons in subantarctic fur seals, *Arctocephalus tropicalis*, on Amsterdam Island, southern Indian Ocean. Growth and survival were studied in relation to year and pup sex, birth date, birth mass, and growth rate at 60 days of age. The pup growth rate decreased over the 7-year study period and was the lowest ever found in otariids, which suggests that lactating females experience constant low food availability. Male and female pups grew and survived at similar rates. Pups that were heavier at birth grew faster and exhibited better early survival (i.e., the first 2 months of life) than pups that were lighter at birth. However, no such relationship was detected for late survival (i.e., from 2 months to weaning) in this long-lactating species. No relationship was found between pup growth rate, pup survival rate, and sea-surface temperature (SST) gradient during the study period, especially during the later years of good trophic conditions (i.e., a high SST gradient). Such dissociations suggest that variation in food availability may not be the only factor influencing pup performance until weaning. We therefore propose that the subantarctic fur seal population is reaching its carrying capacity and that a density-dependent effect is occurring on Amsterdam Island.

Résumé : Les taux de croissance et de survie pré-sevrage des petits de l'otarie à fourrure subantarctique, *Arctocephalus tropicalis*, ont été étudiés pour la première fois durant sept saisons de reproduction consécutives sur l'île Amsterdam. La croissance et la survie ont été mises en relation avec l'année, le sexe, la date de la naissance, la masse à la naissance et le taux de croissance à 60 jours. Durant ces sept années, le taux de croissance des petits a diminué et les valeurs obtenues sont les plus basses rapportées chez les Otaridés, ce qui laisse croire à une disponibilité alimentaire constamment faible pour les femelles nourricières. Mâles et femelles grandissent et survivent à un taux similaire. Les otaries plus lourdes à la naissance grandissent plus vite et survivent mieux que les plus légères au cours des deux premiers mois de leur vie. Cependant, chez cette espèce à allaitement prolongé, la masse à la naissance n'a aucun effet sur la survie de deux mois jusqu'au sevrage. Aucune relation n'a été trouvée durant l'étude entre taux de croissance, taux de survie et gradients de SST (température de surface de la mer), notamment lors des dernières années de bonnes conditions trophiques (fort gradient de SST). Ces dissociations nous amènent à conclure que cette population d'otaries à fourrure subantarctique atteint sa capacité limite et qu'un phénomène de densité-dépendance se produit sur l'île Amsterdam.

[Traduit par la Rédaction]

Introduction

Individual fitness and, to a larger extent, population health can be estimated by measuring the reproductive output of surviving offspring into the next generation (Stearns 1992). The difficulty of obtaining this type of data over long-term studies elucidates the need to use more easily obtained criteria as a proxy of females' reproductive success. In the related literature, these criteria are usually chosen among offspring characteristics (e.g., sex, size, and birth date) and performance (growth rate, weaning mass, and survival rate) during the rearing period (Doidge et al. 1984*b*; Doidge and

Croxall 1989; Baker and Fowler 1992; Lunn et al. 1993; McMahon et al. 2000).

Many studies on seabirds and marine mammals show that interannual variations in breeding success (Cairns 1987; Chastel et al. 1993; Lunn and Boyd 1993*b*; Guinet et al. 1994), offspring growth rate (Doidge et al. 1984*b*; Bester and Van Jaarsveld 1997; Lea and Hindell 1997), and offspring survival (York 1991; Baker and Fowler 1992; Croxall 1992; Barbraud and Weimerskirch 2001) could be related to interannual variations in food-resource availability, in large part because of changes in oceanographic conditions (Trillmich and Ono 1991; Guinet et al. 1998). The last two parameters

M. Chambellant, G. Beauplet,[1] **C. Guinet, and J.-Y. Georges.**[2] Centre d'Études Biologiques de Chizé, Centre National de la Recherche Scientifique, F-79360, Villiers-en-bois, France.

[1]Corresponding author (e-mail: ufuf@cebc.cnrs.fr).

[2]Present address: Centre d'Ecologie et Physiologie Energétiques, Unité Propre de Recherche 9010 du Centre National de la Recherche Scientifique, 23 rue Becquerel, F-67087, Strasbourg, France.

can, however, be affected differently by environmental changes: in pinnipeds, a decrease in pup growth rate has already been observed during moderate El Niño events (e.g., a decrease in food availability), while survival has remained stable in the meantime (see Trillmich and Ono 1991).

The offspring growth rate represents an important factor in animals' life history and many vital parameters are related to and dependent on it (Boltnev et al. 1998). In pinnipeds, especially fur seal species, the pup growth rate during the rearing period reflects the level of maternal input and can be affected by maternal characteristics (e.g., mass and size; Doidge et al. 1984*b*; Mellish et al. 1999; Guinet et al. 2000; Boltnev and York 2001; Bowen et al. 2001), provisioning pattern (Lunn et al. 1993; Georges and Guinet 2000*a*), and experience (Lunn et al. 1994), as well as by pup characteristics (Doidge et al. 1984*b*; Lunn et al. 1993; Boltnev et al. 1998; Guinet et al. 1999; Georges and Guinet 2000*a*).

Offspring survival is one of the major causes of variation in female reproductive success (Lunn et al. 1994; McMahon et al. 2000). In many studies of marine mammals, offspring survival over the entire rearing period has not been investigated, and where it has, results were based on opportunistic counts of dead young (Anderson et al. 1979; Baker 1984; Doidge et al. 1984*a*; Calambokidis and Gentry 1985; Harcourt 1992; Derocher and Stirling 1996; Mison-Jooste 1999; Georges and Guinet 2000*b*). Few studies have investigated factors influencing offspring survival prior to weaning. Birth mass, birth date, size (i.e., length), and weaning mass have been found to be related to offspring survival in some species of marine mammals (northern fur seal, *Callorhinus ursinus*; Boltnev et al. 1998; southern elephant seal, *Mirounga leonina*; McMahon et al. 2000; polar bear, *Ursus maritimus*; Derocher and Stirling 1996). Long-lived species attain their reproductive capacity late, and most marine mammals, such as pinnipeds, experience a high level of dispersion at sea after weaning. A precise estimate of postweaning survival is therefore difficult to obtain. In contrast, preweaning survival is a more accessible measure of offspring survival, as pups remain continuously on the rookery during the entire rearing period.

In this study, changes in pup growth and preweaning survival rates were investigated in subantarctic fur seals, *Arctocephalus tropicalis*, on Amsterdam Island over seven consecutive breeding seasons. Our objectives were to examine the degree to which annual variation, pup characteristics, and pup performance influenced pup growth and survival rates to gain a better understanding of female reproductive success and population trends over time.

Materials and methods

All experimental procedures were conducted according to the ethics and with the scientific approval of the Institut Polaire Paul-Emile Victor Ethics Committee, and complied with the regulations of the Canadian Council on Animal Care.

Study site and animals

The study was carried out at La Mare aux Eléphants breeding colony on the northeast side of Amsterdam Island in the southern Indian Ocean (37°55′S, 77°30′E), where one of the largest breeding colonies can be found (Guinet et al. 1994). This island lies 3000 km from Africa, Australia, and Antarctica and up to 400 km from the subtropical front (STF). The breeding colony was delimited with visual reference markers, allowing us to sample the same portion of the rookery each year from 1995 to 2001.

In subantarctic fur seals, births occur from late November to early January, with a mean parturition date in mid-December (Georges and Guinet 2000*b*). The nursing period lasts about 10 months and pups are weaned from September to November (Tollu 1974; Georges et al. 1999).

Tagging and weighing

The breeding colony was surveyed every day during the parturition period. Within 12 h after birth, each newborn was sexed, weighed (±0.1 kg), and identified by a numbered piece of plastic tape glued to the fur on the top of its head (Georges and Guinet 2000*b*), except in 1998, when field studies began in January. At about 1 month of age each marked pup was tagged on the trailing edge of both foreflippers with an individually numbered plastic tag (Dalton Rototags, Dalton Supply, Nettlebed, U.K.). Each pup-seeking session consisted of a 5-h continuous scan in the delimited rookery section. During these surveys, all tagged pups found were weighed using a rope attached to a spring scale (±0.1 kg). When the mother was present during the weighing of its pup, handling of the pup was undertaken away from her, to minimize disturbance.

In 1995, 1996, and 1999, surveys took place daily throughout the breeding period until October and then twice a week until the end of November (i.e., the end of the weaning period). However, in 1997 and 2001, the colony was checked on 6 days per month (3 consecutive days twice monthly) throughout the breeding period until November. In 1998 and 2000, surveys took place on only 3 consecutive days per month throughout the same period.

Parameters studied

As data collection only began in the first half of January in the 1998 breeding season, and in order to work with similar datasets between years, some of the parameters studied were only investigated from January onwards (at about 30 days of age).

Growth rates

In pinnipeds, pup growth is not positive during the entire rearing period but reaches a maximum and then tends to decrease (Fig. 1). On Amsterdam Island, subantarctic fur seal pups reach their maximum mass in July, at about 230 days of age (Guinet and Georges 2000). The individual global growth rate (GR_G) is defined here as the pup's growth rate from January to when it reached its maximum mass. GR_G was thus estimated by least-square regression of pup body mass on pup age between 30 and 230 days of age (Fig. 1). GR_G was calculated for both sexes for the 7 years of the study.

Another parameter was calculated in order to test the effect of the early pup growth rate (GR_{60}, defined as the growth rate of a pup during its first 2 months of life) on pup survival. Indeed, as all of the pups used to calculate GR_G were still alive at the end of the rearing period, they could not be used

Table 1. Global and early growth rates (GR_G and GR_{60}, respectively) of subantarctic fur seal (*Arctocephalus tropicalis*) pups on

| | 1995 | | 1996 | | 1997 | | 1998 | |
	Males	Females	Males	Females	Males	Females	Males	Females
GR_G (g/d)	**55.3±12.8 (49)**	**48.6±14.8 (56)**	43.2±17.6 (60)	41.4±13.6 (60)	38.3±13.9 (49)	35.0±11.4 (51)	39.5±15.4 (29)	43.9±15.2 (27)
GR_{60} (g/d)	50.8±22.4 (41)	54.0±22.3 (43)	55.2±26.6 (37)	52.1±23.0 (41)	47.0±25.1 (55)	56.5±25.3 (56)	—	—

Note: GR_G is the least-square regression of pup body mass on pup age between 30 and 230 days of age. GR_{60} is the least-square regression of pup body with the sample size in parentheses. Values in boldface type are significantly different between the sexes.

to test for differences in survival. For pups whose birth date and body mass at birth were known, we calculated GR_{60} by least-square regression of body mass on age between 0 and 50–70 days of age (Fig. 1). Only pups with at least four regularly time-spaced body mass measurements within these 2 months were used to calculate GR_{60}. This parameter is the one most commonly used in previous studies investigating pup growth rates in otariids, and is thus suitable for making interspecific comparisons. GR_{60} was calculated for all of the years studied except 1998, as no birth information was available for that breeding season.

Survival rates

The late pup survival rate (SR_L) is defined here as the percentage of pups surviving from 1 month of age until just prior to the weaning process. It was assessed from the mark–recapture history of each individual, using the monthly presence/absence pattern from January to August. Recapture probability was estimated using MARK 1.7 software (White and Burnham 1999) and found to be 94.25 for all years studied. With such a high recapture rate, there was very little chance for a living tagged pup to be missed during a pup-seeking session. Consequently, we did not determine SR_L with a mark–recapture model, but used the following rule instead: a pup that was absent during two consecutive monthly recapture events was considered dead. An associated error was concurrently calculated as the probability of a pup being incorrectly scored as dead (i.e., not observed during 2 consecutive months) when it was not (i.e., it was seen later). SR_L was determined for 5 years. We excluded 1998 and 2000 (when pups were weighed only once a month) from the dataset because data collection was not as regular as in the other years. In these cases, the recapture rate was not suitable for assessing the survival rate.

The early survival rate (SR_E) was concurrently defined as the percentage of pups surviving during their first month of life. It was also calculated from individual pup mark–recapture records from December to February. A pup was determined to be dead if it was absent in February and the following months. SR_E was determined for all years except 1998.

The preweaning survival rate was defined as the percentage of pups surviving from birth until weaning, and was calculated as

$$100 - [(100 - SR_E) + (100 - SR_L)]$$

Oceanographic conditions

During the austral summer, breeding females subantarctic fur seals forage up to 730 km to the southeast of Amsterdam Island (Georges et al. 2000a), mainly near the STF, whose northern and southern limits are defined as the 17.9 and 10.6°C surface isotherms, respectively (Lutjeharms and Val-

entine 1984). The sea-surface temperature (SST) gradient (i.e., change in SST per unit of distance) is an indicator of trophic conditions: the higher the SST gradient, the higher the intensity of its frontal structure and its biological activity (Mann and Lazier 1991). Accordingly, interannual changes in the intensity of the SST gradient were used as a proxy to assess interannual variations in marine productivity. The SST gradient was calculated within a 730 km radius area southeast of Amsterdam Island as follows:

$$SST\ gradient\ (°C\,/\,100\ km) = 17.9 - 10.6°C$$
$$\times\ 100/d_{(N-S)}$$

where $d_{(N-S)}$ is the distance between the northern and southern limits of the STF. In the Amsterdam Island area, a degree of latitude corresponds to 110.8 km. SST measurements were obtained from the Integrated Global Ocean Service System database of the National Ocean and Atmospheric Administration (Reynolds and Smith 1994).

Data analysis

Statistical analyses were performed using Systat 9.0 software (SPSS Inc. 1999). Data were normally distributed. Means were compared using analyses of variance (ANOVA) and then by two-group Student's *t* tests. A general linear model (GLM) was used to test the effects of pup sex, birth date, and birth mass, year, and interactions on GR_G. Each individual in the study was known to be alive or dead from the mark–recapture history. A logistic regression was thus performed to test the effects of pup sex, birth date, birth mass, GR_{60}, year, and interactions on SR_L. SR_L analyses using a logistic regression were only conducted for the 1997 and 1999 breeding seasons, as the sample of dead pups that provided opportunities for calculating GR_{60} was too small to allow analysis of data from the other years. A logistic regression was also run to investigate the effect of pup birth mass on SR_E. SR_E was examined in this way for 1996, 1997, and 1999, as samples from the other breeding seasons were not large enough to allow analysis. A Spearman's rank-correlation analysis was used to test the relationship between the mean SST gradient and either GR_G or SR_L.

All tests were two-tailed and differences were considered significant at $P < 0.05$. Growth rates are given as the mean ± SD with the sample size in parentheses. GLM and logistic regression tables include the contribution and values of significant factors and interactions to the model after stepwise backward analysis.

Results

Pup growth rates

GR_G was estimated for 560 pups during the 7 years of the

Amsterdam Island during the 1995–2001 breeding seasons.

1999		2000		2001		Mean	
Males	Females	Males	Females	Males	Females	Males	Females
35.2±14.0 (19)	35.9±14.8 (38)	44.2±16.3 (24)	38.2±6.1 (32)	25.2±14.7 (30)	28.0±19.1 (32)	41.6±17.2 (260)	39.4±15.1 (296)
29.7±30.8 (29)	34.4±21.9 (43)	47.6±20.0 (10)	38.2±33.2 (10)	62.9±33.8 (25)	44.7±30.5 (24)	48.8±28.1 (197)	48.6±25.8 (217)

mass on pup age between 0 and 60 days of age. GR_{60} was not calculated in 1998 because birth mass was not known. Values are given as the mean ± SD

Fig. 1. Daily changes in mass of subantarctic fur seal (*Arctocephalus tropicalis*) pups on Amsterdam Island. The global growth rate (GR_G) was calculated as the least-square regression of pup body mass on pup age between 30 and 230 days of age. The early growth rate (GR_{60}) was calculated as the least-square regression of pup body mass on age between 0 and 60 days of age.
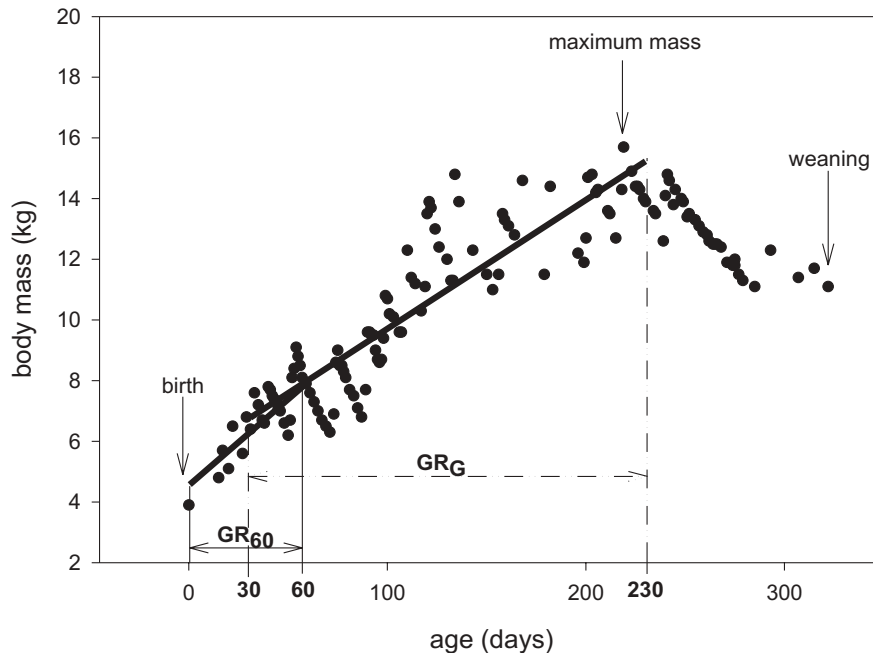
study (Table 1). When birth date and mass at birth for all years combined were considered, we found a positive relationship ($r^2 = 0.018$, $n = 459$, $P = 0.004$). Birth date had a negative effect on GR_G ($t = -9.89$, $n = 460$, $P < 0.001$), and for a given date, pups that were heavier at birth grew faster than pups that were lighter at birth ($t = 2.99$, $n = 460$, $P = 0.003$). A linear regression showed that GR_G decreased significantly ($r^2 = 0.63$, $n = 7$, $P = 0.033$) throughout the study period. Moreover, the mean GR_G differed significantly among years (multivariant analysis of variance (MANOVA), $F_{[13,543]} = 22.8$, $P < 0.001$): a post-hoc Bonferroni test indicated that pups grew fastest in 1995 and experienced the slowest growth rate in 2001 (Fig. 2).

Owing to these differences in GR_G values among years, analyses were then run for each year separately (Table 2). A GLM completed after stepwise backward analysis indicated that in 1995, male pups grew faster than female pups ($t = 2.44$, $n = 105$, $P = 0.016$), but no difference was detected in pup growth rates between the sexes in any of the other years (Table 1). In 1996 and 2000, GR_G was positively correlated with pup birth mass for both sexes (Table 2), whereas in 1995, this correlation was detected only in females ($t = 2.61$, $n = 47$, $P = 0.012$) and not in males ($t = -0.92$, $n = 45$, $P = 0.362$). In 1997, male pups born earlier in the season were found to grow significantly faster ($t = -2.29$, $n = 49$, $P = 0.027$),

but this pattern was not detected for female pups ($t = 0.80$, $n = 51$, $P = 0.426$). In 1998, 1999, and 2001, none of the factors examined were found to have a significant influence on pup GR_G (Table 2).
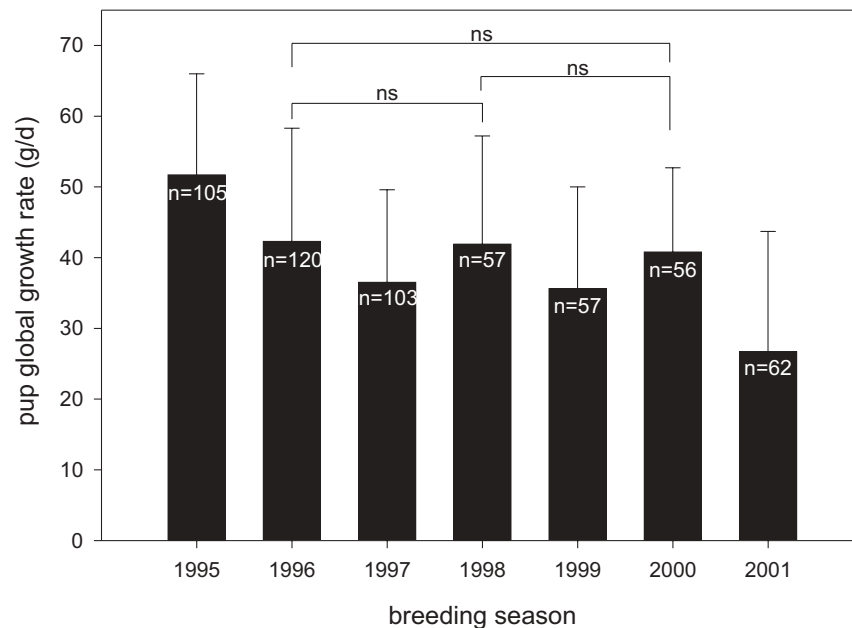
Pup survival rates

SR_E was calculated from 732 pups and ranged from 1% in 2001 to 20.2% in 1999 (Table 3, Fig. 3). When all years were combined, pup birth mass was found to have a positive effect on SR_E (logistic regression, $t = 2.079$, $n = 407$, $P = 0.038$). However, no relationship was found when this analysis was run for each year.

SR_L was determined for 648 pups. A logistic regression showed that the interaction between year and birth date was significant ($t = 3.41$, $P = 0.001$). This implies that birth date could possibly play different roles in determining SR_L depending on the year in question. We therefore conducted logistic regressions for 1997 and 1999 independently.

Neither sex nor birth mass was found to be significant in variations of pup SR_L when data from these years were analyzed separately (Table 4). The interaction between birth date and GR_{60} was significant for both years (Table 4). We therefore divided the birthing period into two sections, before (early) and after (late) the mean birth date (i.e., 12 De-

Fig. 2. Interannual variations in the global growth rate for subantarctic fur seal pups for the 1995–2001 breeding seasons. A Student's *t* test with Bonferroni correction shows the lowest growth rate in 2001 and the highest in 1995. Only nonsignificant (ns) results are identified.

cember), to investigate the effect of GR_{60} on pup survival in each section. In 1997, unlike 1999, the sample of dead pups from which it was possible to calculate GR_{60} for each category (early/late) was large enough to allow us to conduct the analysis. In 1997, preweaning surviving early-born males had a significantly higher GR_{60} ($t = 2.60$, $n = 32$, $P = 0.009$) than those that died before the end of the rearing period (Fig. 4). However, no effect of GR_{60} on preweaning survival has been detected for early-born females ($t = –0.33$, $n = 25$, $P = 0.740$) or late-born pups ($t = –0.89$, $n = 54$, $P = 0.377$).

Oceanographic conditions

The SST gradient at the STF in the southeast region of Amsterdam Island was lowest in 1997 and highest in 1999 (0.636 and 0.698, respectively). Changes in the mean SST gradient throughout the years were not correlated with changes in either GR_G (Spearman's rank correlation, $r_S = –0.27$, $P > 0.05$) or SR_L ($r_S = 0.3$, $P > 0.05$) (Fig. 5).

Discussion

Intraannual variations

Pup growth rates

On Amsterdam Island, GR_G and GR_{60} values for subantarctic fur seal pups are among the lowest ever reported for otariids (see Table 1; Antarctic fur seal, *Arctocephalus gazella*, range 59–108 g·d^{-1}; Lunn and Boyd 1993*b*; Lunn et al. 1993; Guinet et al. 1999; New Zealand fur seal, *Arctocephalus forsterii*, range 58–102 g·d^{-1}; Goldsworthy 1992; Lea and Hindell 1997; *A. tropicalis*, range 81–96 g·d^{-1}; Tollu 1974; Kerley 1985; *C. ursinus*, range 57–72 g·d^{-1}; Gentry and Kooyman 1986; Juan Fernández fur seal, *Arctocephalus philippi*, range 65–82 g·d^{-1}; Ochoa-Acuña et al. 1998; Galápagos fur seal, *Arctocephalus galapagoensis*, range 43–58 g·d^{-1}; Trillmich 1986). The GR_G value is also lower than that previously

found for subantarctic fur seal pups on Amsterdam Island (Guinet and Georges 2000), which indicates a decreasing trend through time in the breeding colony.

Male and female pups grew at similar rates during all breeding seasons except 1995, when males grew significantly faster than females (Table 1). Moreover, the 1995 breeding season showed the highest GR_G value of the 7-year study period, which suggests a year of high food availability (Doidge et al. 1984*b*; Trillmich and Ono 1991; Bester and Van Jaarsveld 1997; Lea and Hindell 1997). This supports Trillmich's (1996) hypothesis that the sex difference in pup growth rates might vary according to environmental factors, such as prey availability (i.e., sex differences were found during years of high prey availability). In fact, the sexes seem to use different growth strategies, male pups preferentially consuming fat while females adopt a fat-conserving pathway (Beauplet et al. 2003). This could explain why male pups take more advantage of bigger fat reserves acquired during years of higher food availability.

Low mean pup growth rates (GR_G and GR_{60}) and the general lack of intersexual differences throughout the study period suggest that subantarctic fur seals breeding on Amsterdam Island were exposed to low food availability during most of these years (Table 1). This is consistent with the extreme attendance pattern among lactating subantarctic fur seals observed on Amsterdam Island, where females perform the longest foraging trips ever recorded in fur seals (Georges and Guinet 2000*a*).

When years were pooled, for a given date, pups that were heavier at birth grew faster than those that were lighter at birth. However, this relationship was found to be significant for both sexes only in 1996 and 2000 and for females only in 1995. Previous studies of otariids have shown a negative relationship (Doidge et al. 1984*b*; Lunn and Boyd 1993*b*; Mison-Jooste 1999) or no relationship (Doidge and Croxall 1989; Georges and Guinet 2000*a*) between birth mass and

Table 2. GLM analysis of pup growth in relation to sex, birth mass, and birth date during the 1995–2001 breeding seasons.

Independent variable	Global growth rate																				
	1995 ($n = 92$)			1996 ($n = 118$)			1997 ($n = 100$)			1998 ($n = 13$)			1999 ($n = 56$)			2000 ($n = 22$)			2001 ($n = 57$)		
	F	df	P	F	df	P	F	df	P	F	df	P	F	df	P	F	df	P	F	df	P
Sex	**5.5**	1	**0.02**	0.3	1	0.59	**4.6**	1	**0.03**	0.03	1	0.87	2.7	1	0.11	1.2	1	0.17	0.7	1	0.39
Birth date	0.3	1	0.55	1.1	1	0.29	2.2	1	0.14	0.3	1	0.59	1.07	1	0.31	1.6	1	0.23	0.03	1	0.87
Birth mass	1.1	1	0.30	**4.0**	1	**0.05**	1.8	1	0.18	0.3	1	0.62	0.1	1	0.73	**10**	1	**0.01**	0.4	1	0.52
Sex × birth date	**5.5**	1	**0.02**	3.3	1	0.07	**4.6**	1	**0.03**	0.03	1	0.87	2.7	1	0.11	0.08	1	0.78	0.7	1	0.39
Sex × birth mass	**7.7**	1	**0.01**	1.8	1	0.05	0.5	1	0.47	0.02	1	0.90	0.5	1	0.47	0.8	1	0.38	0.3	1	0.60

Note: The global growth rate (GR_G) is the dependent variable. Values in boldface type are significantly different after stepwise backward analysis.

pup growth rate. As in other studies, the differences between years that were found here could be due to a variety of variables, such as environmental conditions, species, study sites, and sample size.

Overall, our results showed no clear evidence that any of the factors studied had an effect on GR_G. This could be partly because the mother's size and attendance pattern (i.e., foraging-trip duration and regularity) have been found to play a major role (up to 40%) in variations of pup growth rate within a given year (*A. gazella*; Doidge et al. 1984*b*; Lunn and Boyd 1993*a*, 1993*b*; Lunn et al. 1993; *A. forsterii*; Lea and Hindell 1997; *A. tropicalis*; Georges and Guinet 2000*a*, 2000*b*; Guinet et al. 2000). Our sample may also have been too small year by year to detect any effect of the factors tested.

Pup survival rates

On Amsterdam Island, the mean preweaning survival rate for the subantarctic fur seals (SR_E and SR_L combined) over 5 of the 7 years of the study was 67.7% (Table 3). This result is surely an overestimate, as the preweaning survival rate was calculated from tagged pups, which survived at least during December (i.e., the first 15 days of life): perinatal mortality was thus not considered. However, the range of pup SR_E values found in this study (1–20.2%) is consistent with previous results for otariids (Doidge et al. 1984*a*; Harcourt 1992).

No difference in SR_L values was found between male and female subantarctic fur seal pups on Amsterdam Island. This result is similar to that found for *C. ursinus* (Boltnev et al. 1998) and *U. maritimus* (Derocher and Stirling 1996). However, it is different from previous results found in other highly dimorphic and polygynous mammal species such as ungulates, where young males usually show a higher mortality rate than females (Darwin 1871; Trivers 1972; Clutton-Brock et al. 1985). Those studies, though, dealt with the overall survival rate of young (i.e., pre- and post-weaning survival), so it is possible that an intersexual difference in postweaning survival could occur (Baker and Fowler 1992) in otariids, as their offspring have to face strong constraints after weaning.

On Amsterdam Island, subantarctic fur seal pups that were heavier at birth had a higher SR_E than pups that were lighter at birth, as has previously been found in other fur seal species (Calambokidis and Gentry 1985; Boltnev et al. 1998; Georges and Guinet 2000*b*). However, we found no effect of birth mass on SR_L in this species, which has a long (10 month) lactation period. A possible explanation is that birth mass may play a minor role compared with environmental conditions, as suggested by Baker and Fowler (1992). Similarly, mortality of Antarctic fur seal pups was found to be positively correlated with the foraging-trip duration of their mother (Boyd et al. 1995), which is known to be an indicator of food availability in a given location (Trillmich and Ono 1991; Boyd et al. 1994; Boyd 1999).

Overall, SR_L was positively related to SR_E. When the data were analyzed year by year, this relationship was only found to be significant in 1997 for male pups born before the mean birth date. Georges and Guinet (2000*b*) reported that on Amsterdam Island, SR_E was twice as high for pups born earlier in the breeding season than for those born later. It is also established that in long-lactating fur seal species, larger (i.e.,

Table 3. Early, late, and preweaning mortality rates and preweaning survival rates in subantarctic fur seal pups on Amsterdam Island during the 1995–2001 breeding seasons.

	1995	1996	1997	1999	2001	Mean
n	119	151	190	89	100	648
Early mortality (%)	2.5	3.3	20.1	20.2	1.0	9.4
Late mortality (%)	8.5	18.5	42.5	39.0	11.0	23.9
Late-mortality error (%)	5.0	2.6	4.7	2.2	6.9	4.3
Preweaning mortality (%)	11	21.8	62.6	59.2	12	33.3
Preweaning survival (%)	89.0	78.2	37.4	40.8	88.0	66.7

Note: Early mortality is defined as pup mortality during the first 2 months of life. Late mortality is defined as pup mortality from 2 months to weaning. Preweaning mortality is the sum of early and late mortalities. Preweaning survival is 100 minus preweaning mortality. The error represents the percentage of time a mistake was made in assuming a pup was dead when it was not seen during two consecutive recapture sessions. In the 1998 and 2000 rearing periods, mortality was not calculated, owing to irregular data collection that resulted in a low recapture rate.

Fig. 3. Interannual variations in early and late survival rates for subantarctic fur seal pups for the 1995, 1996, 1997, 1999, and 2001 rearing periods. The 1998 and 2000 breeding seasons were excluded because data collection was not regular and the recapture rate was too low.
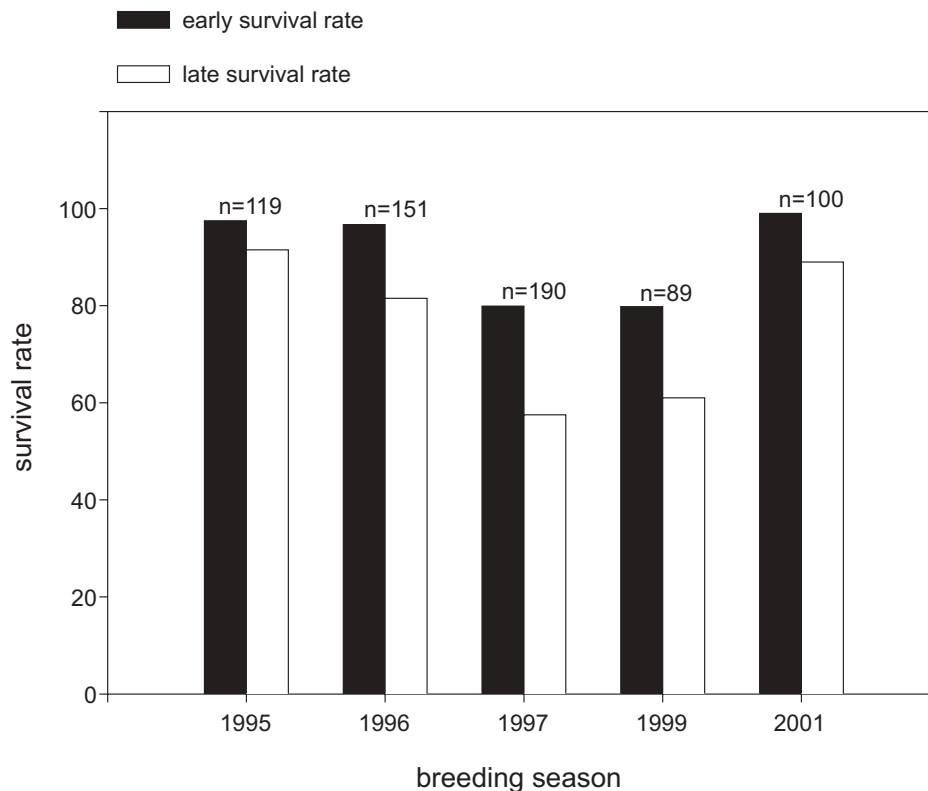

experienced) mothers tended to give birth to heavier pups later during the parturition period (Mison-Jooste 1999; Georges and Guinet 2000b; Guinet et al. 2000). The relationship between GR_{60} and SR_L was found to be not significant in female pups. This suggests that in relation to the sex differences in body composition, growth strategy, and fasting metabolism (Arnould et al. 1996; Beauplet et al. 2003), male pups may be more vulnerable to variation in growth rates.

Interannual variations

Growth and preweaning survival rates of subantarctic fur seal pups were not constant over the 7 years of the study. During this period, however, climatic conditions remained stable, except in February 1998, when tropical storm Anacelle struck the island. Unfortunately, no survival data could have been extracted from the field collection data for that year. Pups raised during the reproductive season of 1995 showed a higher GR_G than those raised during 2001 (Table 1). Although these years may substantially drive this trend, GR_G tended to decrease over the study period. Moreover, this pattern is also confirmed by higher values found in previous studies of this reproductive colony (Tollu 1974; Roux 1986). The preweaning survival rates of subantarctic fur seals ranged from 37.4 to 89.0% (Table 3). These values appear to be lower than those generally found in fur seal studies (Doidge et al. 1984a; Trillmich and Ono 1991) and in

Fig. 4. Early growth rates for early-born male and female subantarctic fur seal pups that died or survived the rearing period in 1997. Early-born pups are those that were born before the mean birth date (12 December). A Student's t test showed that the GR_{60} value for male pups which survived to weaning is higher than for pups that died (***, $P < 0.001$).
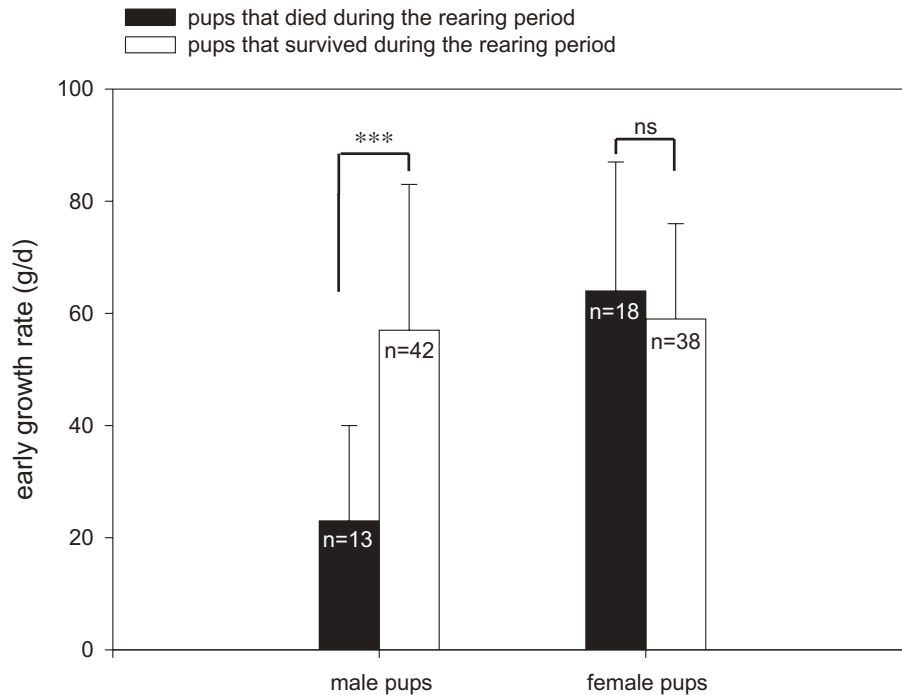
Table 4. Analysis (logistic regression) of pups' late survival rates (SR_L) in relation to sex, birth mass, birth date, and early growth rate (GR_{60}) during the 1997 and 1999 breeding seasons.

| | SR_L | | | |
| | 1997 ($n = 111$) | | 1999 ($n = 66$) | |
	t	P	t	P
Independent variable				
Sex	0.98	0.32	–1.63	0.10
Birth date	**2.58**	**0.01**	**–2.43**	**0.02**
Birth mass	0.73	0.46	–0.03	0.97
GR_{60}	**2.88**	**0.00**	**–1.99**	**0.05**
Birth date × GR_{60}	**–2.88**	**0.00**	**1.99**	**0.05**

Note: SR_L is the dependent variable. Values in boldface type are significantly different after stepwise backward analysis. Analysis of data from the 1995, 1996, 1998, 2000, and 2001 breeding seasons was not possible because the number of dead individuals with a GR_{60} value was too small.

A. tropicalis at Amsterdam Island (Roux 1986). Interannual variability of pup survival and growth rates is usually related to food availability (i.e., abundance and accessibility), which can be determined by the duration of lactating females' foraging trips (Doidge et al. 1984b; York 1991; Trillmich and Ono 1991; Lunn et al. 1993; Boyd et al. 1994; Bester and Van Jaarsveld 1997; Boltnev et al. 1998; Boyd 1999). Our results thus suggest that subantarctic fur seals breeding on Amsterdam Island faced better trophic conditions during the 1995 lactation period than in any of the other years examined. Overall, GR_{60} was higher than GR_G (Table 1). This could be explained by the higher maintenance cost experienced by heavier pups (Guinet et al. 2000). This result also suggests that food availability is globally better during the

austral summer than during the following months, which confirms previous results for fur seals on Amsterdam Island (Georges and Guinet 2000a; Georges et al. 2000b).

The SST-gradient intensity has been shown to be a physical indicator of oceanographic conditions and a priori of trophic conditions (Mann and Lazier 1991). The SST gradient showed some variations during the first years of the study (1995–1998) but remained stable from 1999 to 2001 (Fig. 5). Overall, the decreasing trend in pup growth rate was not related to high pup mortality, and neither of those parameters was related to changes in the SST gradient, especially during the latter years of the study period (Fig. 5). The subantarctic fur seal population on Amsterdam Island is still increasing slightly (unpublished data), which may result in lower prey availability per capita (Bester and Van Jaarsveld 1994). Some lactating females may therefore no longer be able to insure sufficient growth performance for their pups. However, subantarctic fur seal pups have been found to be well adapted to long fasting periods (Beauplet et al. 2003) and are therefore able to endure and survive low growth rates. In a density-dependent situation (i.e., a moderate decrease in food availability), these results could partly be the cause of the dissociation between the growth rate and SR_L, as was found by Trillmich and Ono (1991) during moderate El Niño events. We propose that the subantarctic fur seal population on Amsterdam Island may be reaching its carrying capacity (Guinet and Georges 2000). This phenomenon could thus explain the absence of a relationship between the SST gradient and the studied parameters, which seems to occur especially since 1999 (Fig. 5; a high and constant SST gradient, suggesting favourable trophic conditions, but a decreasing and unstable GR_G). The general model of population autoregulation states that variation in the survival of

Fig. 5. Changes in the mean sea surface temperature (SST) gradient at the subtropical front southeast of Amsterdam Island and global growth rates (GR_G) for subantarctic fur seal pups throughout the 7 years of the study (*a*) and late survival rates (SR_L) for subantarctic fur seal pups for the 1995, 1996, 1997, 1999, and 2001 breeding seasons (*b*). The 1998 and 2000 rearing periods were excluded because data collection was not regular and the recapture rate was low.
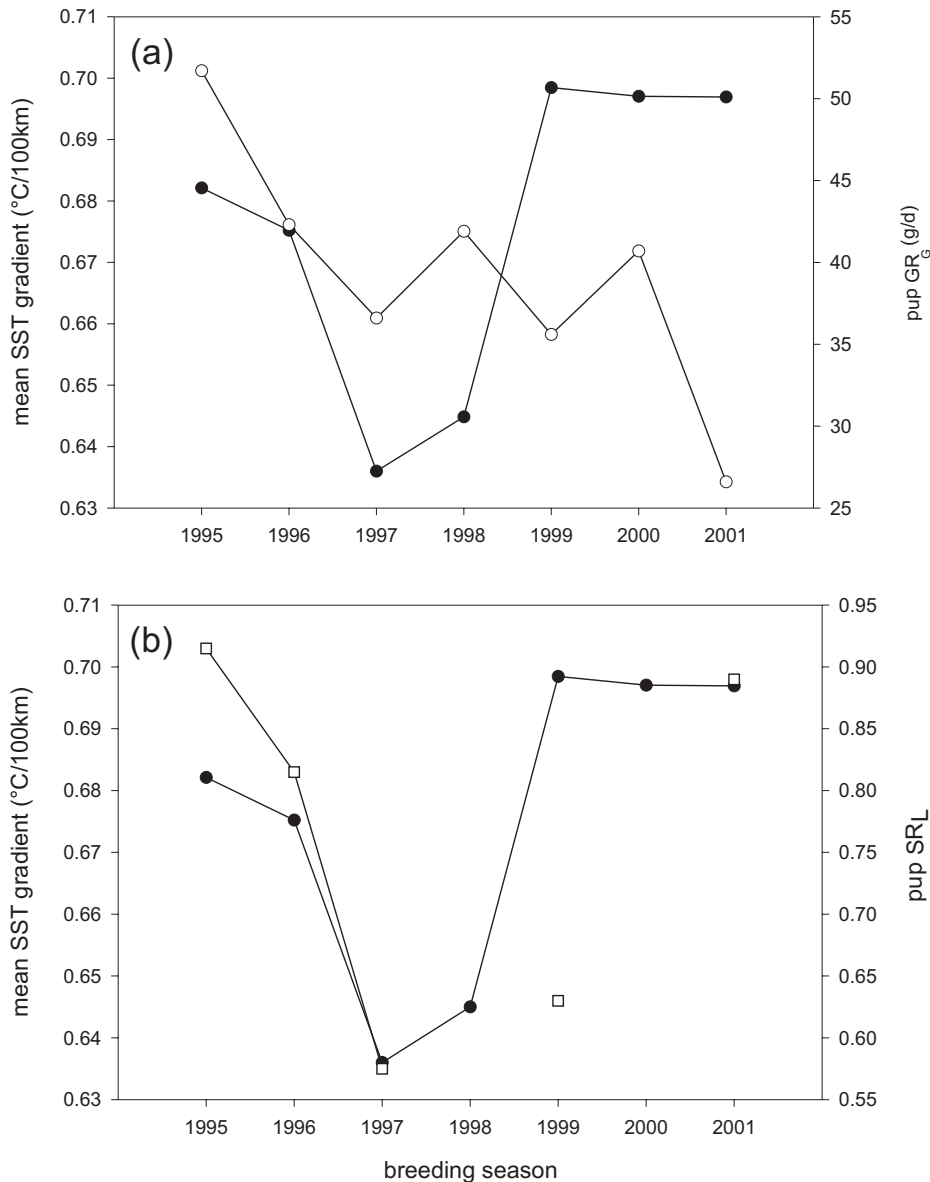
young is one of the major causal factors involved (Eberhardt 1977). A low pup growth rate should indeed affect the mass at weaning, which is known to be critical for future pup survival (Baker and Fowler 1992; Boltnev et al. 1998; McMahon et al. 2000). In fact, pups born during the breeding season of 2001 exhibited the lowest weaning mass found throughout the 7 years of the study (unpublished data). Consequently, although preweaning survival was not density-dependent, one might expect pups to experience particularly low postweaning survival rates during that year.

Acknowledgments

References

Anderson, S.S., Baker, J.R., Prime, J.H., and Baird, A. 1979. Mortality in grey seal pups: incidence and causes. J. Zool. (1965–1984), **189**: 407–417.

Arnould, J.P.Y., Boyd, I.L., and Socha, D.G. 1996. Milk consumption and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups. Can. J. Zool. **74**: 254–266.

Baker, J.D., and Fowler, C.W. 1992. Pup weight and survival of northern fur seals *Callorhinus ursinus*. J. Zool. (Lond.), **227**: 231–238.

Baker, J.R. 1984. Mortality and morbidity in grey seal pups (*Halichoerus grypus*): studies on its causes, effects of environment, the nature and sources of infectious agents and the immunological status of pups. J. Zool. (1965–1984), **203**: 23–48.

Barbraud, C., and Weimerskirch, H. 2001. Emperor penguins and climate change. Nature (Lond.), **411**: 183–186.

Beauplet, G., Guinet, C., and Arnould, J.P.Y. 2003. Body composition changes, metabolic fuel use and energy expenditure during extended fasting in subantarctic fur seal (*Arctocephalus tropicalis*) pups at Amsterdam Island. Physiol. Biochem. Zool. **76**: 262–270.

Bester, M.N., and Van Jaarsveld, A.S. 1994. Sex-specific and latitudinal variance in postnatal growth of the subantarctic fur seal (*Arctocephalus tropicalis*). Can. J. Zool. **72**: 1126–1133.

Bester, M.N., and Van Jaarsveld, A.S. 1997. Growth in the subantarctic fur seal *Arctocephalus tropicalis* pups as possible indicator of offshore food availability. *In* Marine mammal research in the southern hemisphere: status, ecology and medicine. *Edited by* M.A. Hindell and C. Kemper. Surrey Beatty, Chipping Norton, N.S.W., Australia. pp. 88–91.

Boltnev, A.I., and York, A.E. 2001. Maternal investment in northern fur seals (*Callorhinus ursinus*): interrelationships among mothers' age, size, parturition date, offspring size and sex ratios. J. Zool. (Lond.), **254**: 219–228.

Boltnev, A.I., York, A.E., and Antonelis, G.A. 1998. Northern fur seal young: inter-relationships among birth size, growth, and survival. Can. J. Zool. **76**: 843–854.

Bowen, W.D., Iverson, S.J., Boness, D.J., and Oftedal, O.T. 2001. Foraging effort, food intake and lactation performance depend on maternal mass in small phocid seal. Funct. Ecol. **15**: 325–334.

Boyd, I.L. 1999. Foraging and provisioning in Antarctic fur seals: interannual variability in time energy budgets. Behav. Ecol. **10**: 198–208.

Boyd, I.L., Arnould, J.P.Y., Barton, T., and Croxall, J.P. 1994. Foraging behaviour of the Antarctic fur seal during periods of contrasting prey abundance. J. Anim. Ecol. **63**: 703–713.

Boyd, I.L., Croxall, J.P., Lunn, N.J., and Reid, K. 1995. Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. J. Anim. Ecol. **64**: 505–518.

Cairns, D.K. 1987. Seabirds as indicators of marine food supplies. Biol. Oceanogr. **5**: 261–271.

Calambokidis, J., and Gentry, R.L. 1985. Mortality of northern fur seal pups in relation to growth and birth weights. J. Wildl. Dis. **21**: 327–330.

Chastel, O., Weimerskirch, H., and Jouventin, P. 1993. High annual variability in reproductive success and survival of an Antarctic seabird, the snow petrel *Pagodroma nivea*. Oecologia, **94**: 278–285.

Clutton-Brock, T.H., Guinness, F.E., and Albon, S.D. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. Nature (Lond.), **313**: 131.

Croxall, J.P. 1992. Southern ocean environmental changes: effects on seabird, seal and whale populations. Philos. Trans. R. Soc. Lond. B Biol. Sci. **338**: 319–328.

Darwin, C. 1871. The descent of man and selection in relation to sex. John Murray, London.

Derocher, A.E., and Stirling, I. 1996. Aspects of survival in juvenile polar bears. Can. J. Zool. **74**: 1246–1252.

Doidge, D.W., and Croxall, J.P. 1989. Factors affecting weaning weight in Antarctic fur seals *Arctocephalus gazella* at South Georgia. Polar Biol. **9**: 155–160.

Doidge, D.W., Croxall, J.P., and Baker, J.R. 1984*a*. Density-dependent pup mortality in the Antarctic fur seal *Arctocephalus gazella* at South Georgia. J. Zool. (1965–1984), **202**: 449–460.

Doidge, D.W., Croxall, J.P., and Ricketts, C. 1984*b*. Growth rates of Antarctic fur seal *Arctocephalus gazella* pups at South Georgia. J. Zool. (1965–1984), **203**: 87–93.

Eberhardt, L.L. 1977. Optimal policies for conservation of large mammals with special reference to marine ecosystems. Environ. Conserv. **4**: 205–212.

Gentry, R.L., and Kooyman, G.L. 1986. Fur seals: maternal strategies on land and at sea. Princeton University Press, Princeton, N.J.

Georges, J.-Y., and Guinet, C. 2000*a*. Early mortality and perinatal growth in the subantarctic fur seals *Arctocephalus tropicalis* on Amsterdam Island. J. Zool. (Lond.), **251**: 277–287.

Georges, J.-Y., and Guinet, C. 2000*b*. Maternal care in the subantarctic fur seals on Amsterdam Island. Ecology, **81**: 295–308.

Georges, J.-Y., Sevot, X., and Guinet, C. 1999. Forstering in a subantarctic fur seal. Mammalia, **63**: 384–388.

Georges, J.Y., Bonadonna, F., and Guinet, C. 2000*a*. Foraging habitat and diving activity of lactating subantarctic fur seals in relation to sea surface temperatures on Amsterdam Island. Mar. Ecol. Prog. Ser. **196**: 291–304.

Georges, J.Y., Tremblay, Y., and Guinet, C. 2000*b*. Seasonal diving behaviour in lactating subantarctic fur seals on Amsterdam Island. Polar Biol. **23**: 59–69.

Goldsworthy, S.D. 1992. Maternal care in three species of southern fur seals (*Arctocephalus* spp.) Ph.D. thesis, Monash University, Melbourne.

Guinet, C., and Georges, J.-Y. 2000. Growth in pups of the subantarctic fur seal (*Arctocephalus tropicalis*) on Amsterdam Island. J. Zool. (Lond.), **250**: 289–296.

Guinet, C., Jouventin, P., and Georges, J.-Y. 1994. Long term population changes of fur seals *Arctocephalus gazella* and *Arctocephalus tropicalis* on subantarctic (Crozet) and subtropical (St Paul and Amsterdam) islands and their possible relationship to El Niño Southern Oscillation. Antarct. Sci. **6**: 473–478.

Guinet, C., Chastel, O., Koudil, M., Durbec, J.P., and Jouventin, P. 1998. Effects of warm sea-surface temperature anomalies on the blue petrel at Kerguelen Islands. Proc. R. Soc. Lond. B Biol. Sci. **265**: 1001–1006.

Guinet, C., Goldsworthy, S.D., and Robinson, S. 1999. Sex differences in mass loss rate and growth efficiency in Antarctic fur seal (*Arctocephalus gazella*) pups at Macquarie Island. Behav. Ecol. Sociobiol. **46**: 157–163.

Guinet, C., Lea, M.-A., and Goldsworthy, S.D. 2000. Mass change in Antarctic fur seal (*Arctocephalus gazella*) pups in relation to maternal characteristics at the Kerguelen Islands. Can. J. Zool. **78**: 1–8.

Harcourt, R. 1992. Factors affecting early mortality in the South American fur seal (*Arctocephalus australis*) in Peru: density-related effects and predation. J. Zool. (Lond.), **226**: 259–270.

Kerley, G.I.H. 1985. Pup growth in the fur seals *Arctocephalus tropicalis* and *A. gazella* on Marion Island. J. Zool. Ser. A, **205**: 315–324.

Lea, M.-A., and Hindell, M.A. 1997. Pup growth and maternal care in New Zealand fur seals, *Arctocephalus forsteri*, at Maatsuyker Island, Tasmania. Wildl. Res. **24**: 307–318.

Lunn, N.J., and Boyd, I.L. 1993*a*. Effects of maternal age and condition on parturition and the perinatal period of Antarctic fur seals. J. Zool. (Lond.), **229**: 55–67.

Lunn, N.J., and Boyd, I.L. 1993*b*. Influence of maternal character-istics and environmental variation on reproduction in Antarctic fur seals. Symp. Zool. Soc. Lond. No. 66. pp. 115–129.

Lunn, N.J., Boyd, I.L., Barton, T., and Croxall, J.P. 1993. Factors affecting the growth weight and mass at weaning of Antarctic fur seals at Bird Island, South Georgia. J. Mammal. **74**: 908–919.

Lunn, N.J., Boyd, I.L., and Croxall, J.P. 1994. Reproductive perfor-mance of female Antarctic fur seals: the influence of age, breed-ing experience, environmental variation and individual quality. J. Anim. Ecol. **6**: 827–840.

Lutjeharms, J.R.E., and Valentine, H.R. 1984. Southern Ocean thermal fronts south of Africa. Deep-Sea Res. **31**: 1461–1475.

Mann, K.H., and Lazier, J.R.N. 1991. Dynamics of marine ecosys-tems, biological–physical interactions in the ocean. Blackwell Scientific Publications, Oxford.

McMahon, C.R., Burton, H.R., and Bester, M.N. 2000. Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. Antarct. Sci. **12**: 149–153.

Mellish, J.-A.E., Iverson, S.J., and Bowen, W.D. 1999. Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. Physiol. Biochem. Zool. **72**: 677–690.

Mison-Jooste, V. 1999. Contribution à l'étude de la biologie des populations de l'otarie à fourrure du Cap (*Arctocephalus pusillus pusillus*) : les soins maternels diffèrent-ils en fonction du sexe du jeune? Ph.D. thesis, Université de Lyon 1, Lyon, France.

Ochua-Acuña, H., Francis, J.M., and Boness, D.J. 1998. Interannual variation in birth mass and postnatal growth rate of Juan Fernández fur seals. Can. J. Zool. **76**: 978–983.

Reynolds, R.W. and Smith, T.M. 1994. Improved global sea sur-face temperature analyses. J. Climatol. **7**: 929–948. Available from http://ingrid.ldgo.columbia.edu (accessed on September 2002).

Roux, J.P. 1986. Sociobiologie de l'otarie *Arctocephalus tropicalis*. Ph.D. thesis, Université des Sciences et Techniques du Languedoc, Montpellier, France.

Stearns, S.C. 1992. The evolution of life histories. Oxford Univer-sity Press, Oxford.

SPSS Inc. 1999. Systat ver. 9.0. SPSS Inc., Chicago.

Tollu, B. 1974. L'otarie de l'île d'Amsterdam *Arctocephalus tropicalis* (Gray 1872). Ph.D. thesis, Université de Paris 7, Paris, France.

Trillmich, F. 1986. Maternal investment and sex-allocation in the Galapagos fur seal, *Arctocephalus galapagoensis*. Behav. Ecol. Sociobiol. **19**: 157–164.

Trillmich, F. 1996. Parental investment in pinnipeds. Adv. Stud. Behav. **25**: 533–577.

Trillmich, F., and Ono, K.A. (*Editors*). 1991. Pinnipeds and El Niño: responses to environmental stress. Springer-Verlag, Berlin and Heidelberg.

Trivers, R.L. 1972. Parental investment and sexual selection. *In* Sexual selection and the descent of man. *Edited by* B. Campbell. Aldine, Chicago. pp. 136–149.

White, G.C., and Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study, **46**(Suppl.): S120–S139.

York, A.E. 1991. Sea surface temperatures and their relationship to the survival of juvenile male northern fur seals from the Pribilof Islands. *In* Pinnipeds and El Niño. Chap. 9. *Edited by* F. Trillmich and K.A. Ono. Springer-Verlag, Berlin and Heidelberg.