

Age structure, growth, and demographic parameters in breeding-age female subantarctic fur seals, *Arctocephalus tropicalis*

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Abstract: Age distribution was estimated for 108 breeding-age female subantarctic fur seals, *Arctocephalus tropicalis* (Gray, 1872), sampled during the 1999–2000 breeding season on Amsterdam Island, southern Indian Ocean. The growth features were described and demographic parameters assessed from transversal life tables constructed for this female population. The breeding females had a longer mean body length than was observed for other breeding populations of the same species. These females also showed a later start to reproduction (6 years old), a lower overall age-specific reproductive rate ($R_{6-16} = 48.0\%$), and a lower survival in older age classes (>13 years). Females reproduced up to a maximum age of 16 years, with none older than 19 years observed in the colony, suggesting an apparent senescence in the population. This consequently reduced the theoretical reproductive period of the females, which has led to a lower number of reproductive outputs per individual (i.e., 3.65 weaned pups per female throughout its reproductive life). Although such differences between islands may be related to genotypic traits, these results are consistent with low food availability and suggest that density-dependent regulatory processes operate on the Amsterdam Island population.

Résumé : La structure en âge a été estimée chez 108 femelles otaries à fourrure subantarctique, *Arctocephalus tropicalis* (Gray, 1872), en âge de reproduction et échantillonnées au cours de la saison de reproduction 1999–2000 sur l'île d'Amsterdam dans le sud de l'Océan Indien. La croissance a été décrite et les paramètres démographiques estimés à partir des tables de données transversales de cette population de femelles. Les femelles reproductrices ont une longueur corporelle moyenne supérieure à celle observée chez d'autres populations de la même espèce. Elles ont aussi une entrée tardive à la reproduction (6 ans), un taux de reproduction inférieur ($R_{6-16} = 48,0\%$) et une survie inférieure dans les classes d'âge avancées (>13 ans). Ces femelles se reproduisent jusqu'à un âge maximal de 16 ans et aucune femelle plus vieille que 19 ans n'a été observée dans la colonie, ce qui indique une sénescence apparente de la population. Ceci a pour conséquence de diminuer la période théorique de reproduction des femelles, menant à un nombre inférieur de petits produits par individu (i.e. 3,65 petits sevrés par femelle au cours de sa vie reproductrice). Même si ces différences entre populations insulaires peuvent être liées à des traits génétiques, ces résultats sont cohérents avec une faible disponibilité alimentaire et laissent supposer que des phénomènes de densité-dépendance se produisent chez la population de l'île d'Amsterdam.

Introduction

Tremendous differences in demographic parameters exist among living organisms (Stearns 1992). For instance, fundamental key parameters such as life span and the number of reproductive events are highly variable depending on the studied species (Stearns 1992). This diversity is probably related to the different constraints and selective pressures experienced by a population. Notably, each species exhibits a

specific trade-off regarding growth, reproduction, and survival features (Stearns 1992). To understand this trade-off, it is necessary to precisely describe how these parameters vary with age throughout the life of the studied organism. Crucial information such as age-specific survival and reproductive rates are necessary to assess demographic parameters like the successive reproductive steps (Harwood and Prime 1978; Dajoz 1996), growth rate, life span, age structure, and consequently, the reproductive value of the studied population (Klevezal and Kleinenberg 1969; Boyd et al. 1990; Pough et al. 1999). Ultimately, the resulting individual growth, reproductive, and survival patterns are dependent on natural selection, and thus, may theoretically optimize the fitness of the animal (Stearns 1992). This optimization of demographic parameters may vary in response to specific environmental constraints (Newton 1998).

To better understand the influence of environmental constraints on adaptive trade-offs, it is pertinent to use models that exist in diverse geographic zones, and consequently, facing many different environmental conditions (i.e., climate, food). In this context, pinnipeds represent a group of major interest, as the individual age can be determined by counting tooth growth layer groups (GLGs), assuming the layered

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pattern of the recording structure is the result of an annual periodicity in growth (Scheffer 1950; Laws 1952; Perrin and Myrick 1980). In the course of their reproductive lives, pinnipeds regularly attend at their reproductive site (Gentry and Kooyman 1986), which allows scientists to obtain regular access to biological information. While males invest only a short period of time in reproduction, maternal investment is very high and often includes a period of caring for young, which can be extended considerably in some otariid species (Trillmich 1996).

The subantarctic fur seal, *Arctocephalus tropicalis* (Gray, 1872), is characterized by specific traits, and their breeding sites are located on a diverse array of islands in the southern oceans (Wickens and York 1997), with populations facing highly different dynamics and environmental conditions (Chivers 2002). On Amsterdam Island (southern Indian Ocean), however, the foraging strategy during reproduction seems to be among the most extreme observed in this fur seal species, with extended foraging trips and low pup growth rates (Chambellant et al. 2003; Beauplet et al. 2004). It is thus of major interest to examine whether these extreme conditions affect the main demographic parameters of this population, and to make a comparison with other fur seal species breeding perhaps under more favourable environmental conditions.

The aims of this study were, therefore, to (i) determine the age distribution of the reproductive female population, (ii) assess female age at sexual maturity and reproductive life span, (iii) assess age-specific reproductive rate, and (iv) describe the growth of the female subantarctic fur seals breeding on Amsterdam Island.

Materials and methods

All experimental procedures were approved by the Institut Polaire Paul-Emile Victor (IPEV) 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 Elephants colony on the northeastern side of Amsterdam Island (35°55'S, 77°30'E), southern Indian Ocean, where one of the largest breeding colonies of *A. tropicalis* can be found (Guinet et al. 1994). This colony consists of an "established breeding colony" (i.e., 80% surface-area coverage of the breeding ground) that is surrounded by a 20% surface-area strip of "breeding colony" type (see Bester 1982). This population is situated on an intermediate beach type (see Bester 1982) and has reached phase IV (i.e., maturity) of the recolonization process (see Roux 1987; Chambellant et al. 2003; Beauplet et al. 2004; G. Beauplet and C. Guinet, unpublished data).

In subantarctic fur seals, mean parturition date occurs at mid-December (Georges and Guinet 2001) and the pup-rearing period lasts about 10 months (Kerley 1985). Each year since the 1993–1994 breeding season, 100–150 pups were tagged on the trailing edge of both foreflippers with an individually numbered plastic tag (Dalton Rototags, Dalton

Supply, Nettlebed, UK). Searches for tagged subantarctic fur seals were conducted every 2 days in the colony during the 1995–2003 breeding seasons (Chambellant et al. 2003), which allowed us to observe the postweaning return of animals of known age (Beauplet et al.).² In this study, we defined a breeding female as a female giving birth to a pup during a given season, whereas reproductive females consisted of females that have bred at least once during their life.

Field procedures

Morphometric data and tooth samples were collected from 108 free-ranging reproductive female subantarctic fur seals during autumn and winter of 1999. Nonbreeding females (i.e., no pup attendance and depleted mammary glands, $n = 23$) were caught opportunistically in the colony, while the breeding ones ($n = 85$) were caught just after their return from a foraging trip (see Dabin et al. 2002). A satisfactory level of anaesthesia was used to complete a tooth extraction on each animal (Dabin et al. 2002). Females were held in a prone position on a restraint board (Gentry and Kooyman 1986), and the individual standard body length (± 1 cm) was measured ventrally as the straight line from the snout to the tail tip. This method permits comparison with any study measuring snout–tail length of female fur seals.

Prior to the extraction, the mouth was kept open and immobilized using a soft wooden block and the teeth and gums situated around the tooth to be extracted were cleaned with an antiseptic solution (Vétédine® 0.02% v/v; Vétéquinol, 70204 Lure CEDEX, France). The lower left postcanine 1 was then removed within a few minutes, using a dental elevator (Cottrel & Compagnie, Charlotte Street, London, W1P2AA, UK), as described in Arnbom et al. (1992). To prevent haemorrhaging and infection, the empty alveolus was then cleaned with Vétédine® before placing an adhesive antiseptic diffuser (Stomadhex C300; Vétéquinol, 70204 Lure CEDEX, France) into the root cavity. Each removed tooth was cleaned, labelled, and then stored in 70% glycerinated alcohol (Nielsen 1972; Perrin and Myrick 1980).

Teeth preparation and age determination

Individual ages were estimated from counts of incremental growth layers in the dentine of tooth sections (Arnbom et al. 1992; Bester 1995). To investigate the accuracy of our age estimates, the GLGs' deposition pattern was estimated from two different preparation methods, as well as using tagged individuals of known age ($n = 3$, range 3–5 years of age) as recommended in previous studies (Nielsen 1972; Perrin and Myrick 1980; Hohn and Fernandez 1999). In the first method (the undecalcified method), unstained thin sections of teeth were prepared by grinding (Perrin and Myrick 1980). These undecalcified sections were polished with whetstones (1200 and 4000 grit) and then mounted in a synthetic Epoxy resin (Strueurs S.A.; Z.I. du parc, BP 114 Noisy le Sec, France). In the second method (the decalcified method), the tooth sections were first placed in a decalcifying agent (DC3 Labonord®; Z.I. de Templemars, F-59175 Tem-

²G. Beauplet, C. Barbraud, M. Chambellant, and C. Guinet. 2004. Interannual variations of post-weaning survival in subantarctic fur seals: influence of pup sex, growth rate, and environmental conditions. Submitted manuscript.

plemars, France), washed overnight in running water, and finally mounted in a synthetic medium (Isomount Labonord®; Z.I. de Templemars, F-59175 Templemars, France) (see Perrin and Myrick 1980).

The tooth sections were examined under a stereomicroscope with transmitted polarized light (Olympus® BH2; Olympus Optical Co., Tokyo, Japan) to count GLGs, assuming that 1 GLG represents a whole-year period as demonstrated for this and other otariid species (Anas 1970; Arnbom et al. 1992; Rosas et al. 1993; Bester 1995). Considering that the deposition of the yearly GLG border usually occurs during mid- to late summer (Dickie and Dawson 2003), the starting point of our age determination was defined as the median birth date for the colony. The seals captured in this study were sampled during the fall, and thus, have started a new GLG at that time, which allowed us to estimate an incomplete GLG as a fraction of a complete GLG (e.g., 12.3 years; see Hohn and Lockyer 1995).

Using both methods outlined above, two independent readers performed three counts recorded to the nearest whole year, which then was used to provide a mean (\pm SD) age for each individual. To determine the best age-determination procedure, reading variability was compared between both readers and both methods, and was also assessed by the exact age estimates obtained from the animals of known age. The two readers agreed to use the decalcified tooth age-estimate method, as there was significantly less reading variability between the two readers when this method was used over the undecalcified tooth method (decalcified method, $F_{[1,107]} = 1.376$, $P > 0.05$; undecalcified method, $F_{[1,107]} = 3.975$, $P < 0.05$). The majority of the within-reader differences was due to the rounding error to the nearest whole year, which confirmed that the decalcified tooth method allowed for a more accurate description of the age distribution of the reproductive female subantarctic fur seal population on Amsterdam Island.

Growth curve

In mammals, the body growth pattern usually has a sigmoidal shape with an asymptotic trend and has frequently been described as fitting nonlinear models (Turner et al. 1976; Zullinger et al. 1984; McLaren and Smith 1985). The Gompertz growth curve represents a standard curve that is commonly known to best describe mammalian growth (Laird 1966; Heide-Jorgensen and Teilmann 1994), especially in pinnipeds (York 1983; Hammill et al. 1995). Hence, we described here the female subantarctic fur seal growth using the Gompertz growth curve, which is defined by the following equation (Sugden et al. 1981; Hammill et al. 1995):

$$L(t) = AL e^{\{-e^{[-e^{k(t-t_0)}]}\}}$$

where $L(t)$ is the length (cm) at age t (year), AL is the animal's asymptotic body length (cm), k is the maximum relative growth rate (year^{-1}), and t_0 is the age (year) when the maximum growth rate occurs (Sugden et al. 1981). We reparameterized this equation to its basic form:

$$L(t) = AL e^{(-ae^{-bt})}$$

where a and b are fitting constants.

Using Microsoft® Excel Stat version 5.1, the age-length relationship of the study population was fitted to the data for 108 females using one fixed parameter for the mean body length at birth (mean BL = 60.5 cm; see Georges and Guinet 2001).

Reproductive rate

During the regular searches for tagged subantarctic fur seals, we recorded the tag number and breeding status of each female of known age, i.e., an individual that had been either tagged as a pup (see Chambellant et al. 2003) or caught for a tooth extraction (this study). These additional observations allowed us to significantly increase the sample size of the younger age classes (i.e., 3–6 years of age) and also to obtain information on older age classes than that observed in 1999 (e.g., seals of 15 years of age as determined in 1999 belong to the 19-year-old age class in 2003). As a result, this will enable us to obtain a more complete description of the reproductive rate by age class of the reproductive female population where R_X (%) represents the percentage of tagged breeding females of age class X .

Results

Growth curves

The female age – body length relationship using the Gompertz growth model was best described by the following equation (Fig. 1):

$$L(t) = 141.0 e^{(-0.86 e^{-0.43t})} \quad (r^2 = 0.85)$$

The Gompertz model estimated the female's body length as having an asymptotic trend ($AL = 141.0$ cm) beyond 12 years of age (Fig. 1), which allowed us to define the starting point of the physical maturity phase (Chivers 2002). Individuals older than 3 years of age showed a body length of 111.3 cm (Fig. 1). The exponential growth phase of the Gompertz curve, commonly used to define the sexual maturation phase of mammals (Pitcher and Calkins 1981; Laws and Sinha 1993), occurred in the 3- to 8-year-old age group (Fig. 1). In this age group, mean body length was 134.6 ± 1.0 cm, and the youngest reproductive female was 5 years of age (Fig. 3), with a length at first reproduction (LAFR) of 127.6 cm (Table 1). Overall, the mean body length of the breeding females sampled during the 1999–2000 breeding season was 136.6 cm (Table 1).

Age distribution obtained from the 1999 breeding season

The age distribution (i.e., P_X (%) represents the percentage of tagged females of age class X) of the sampled reproductive female's population extended from 3 to 15 years of age, with an observed mean of 9.2 ± 0.2 years of age (Fig. 2). This distribution presented a gaussian shape, with a mode occurring from 7 to 10 years of age ($P_{7-10} = 64.8\%$), and a most common age class of 8 years ($P_8 = 19.4\%$). However, 22.2% of the animals were older than 10 years of age, with a secondary peak in frequency evident at 14 years of age (Fig. 2). The lowest age classes represented the smallest part of the sampled population ($P_{3-6} = 13.0\%$) and

Fig. 1. Gompertz growth curve fitted to age-specific standard body length in breeding female subantarctic fur seals, *Arctocephalus tropicalis* ($n = 108$). (a) Growth during the sexual maturation phase (3–8 years). (b) Asymptotic length attainment (8–11 years). (c) Physical maturation phase (>11 years). AFR, age (years) at first reproduction; LAFR, length (cm) at first reproduction; AL, asymptotic length (cm); AAL, age (years) at asymptotic length; ASM, age (years) at sexual maturity. Demographic parameters estimated as follows: AFR = 5 years, LAFR = 127.6 cm, ASM = 3–5 years, AAL = 11.2 years, and AL = 141.0 cm.

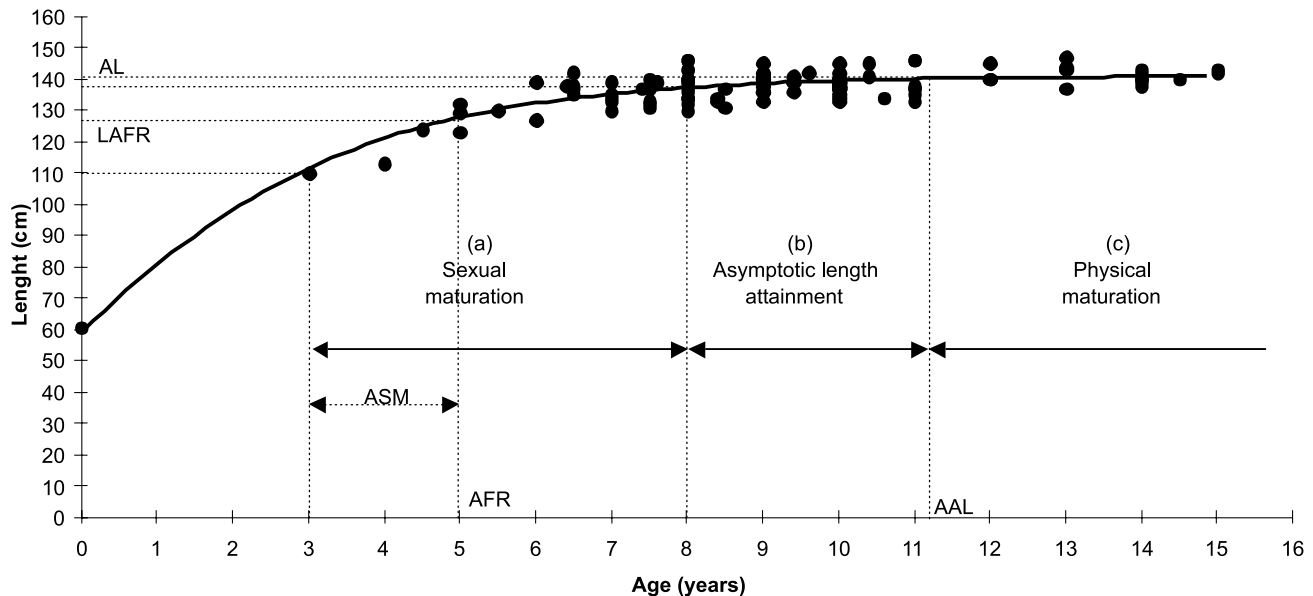


Table 1. Comparison of body length (mean \pm SD) between reproductive adult female subantarctic fur seals, *Arctocephalus tropicalis*, from different island populations.

Island	Body length (cm)	n	Range		Source
			LAFR (cm)	AL (cm)	
Amsterdam	136.6 \pm 0.9	108	127.6	141.0	This study
Gough	122.3 \pm 6.0	64	104.3	132.0	Bester and Van Jaarsveld 1994
Marion	120.5 \pm 4.6	7	112.5	126.6	Bester and Van Jaarsveld 1994
Crozet	117.3 \pm 6.2	75	102.5	133.0	S. Luque, unpublished data

Note: LAFR is body length at first reproduction and AL is asymptotic body length. Values in Gough, Marion, and Crozet islands were estimated as the minimum and maximum body lengths measured in breeding females from each study site.

showed an exponential increase between 3 and 6 years of age (Fig. 2). In the total sampled population ($n = 108$), 78.7% of the females had a reproductive status, with a minimum age at reproduction of 6 years of age.

Reproductive rate

When including individuals that had been tagged as pups in the analysis, some females appeared to start reproduction at 5 years of age ($R_5 = 2.4\%$; Fig. 3). Age-specific breeding rate was still low at 6 years of age ($R_6 = 6.1\%$), but then dramatically increased to reach a maximum for the 8- to 13-year-old age classes ($R_{8-13} = 62.7\%$; Fig. 3). This most productive age group represented 66.6% of the females sampled (see Fig. 2), with the 12-year-old age class constituting the maximum reproductive rate ($R_{12} = 72.1\%$) of the females (Fig. 3). This was followed by a steady decrease in reproductive rates from 0.40–0.47 at 14–15 years of age ($n = 39$) to 0.25 at 16 years of age ($n = 12$). No female was observed to produce a pup after 16 years of age ($n = 16$; Fig. 3). Overall, this age-specific reproductive rate was best fitted by a second-order polynomial relationship (Fig. 3). The overall reproductive rate for >5-year-old females was 48.0%.

Discussion

Growth and reproductive rates

First, it is notable that the proportion of reproductive females (Fig. 2) showed a skewed distribution toward the younger age classes (i.e., <6 years of age) of the population. Yet our sampling protocol primarily was aimed at sampling the whole range of body-length classes among the reproductive female population, which then allowed us to obtain a random sample of the breeding population, including the younger age classes where females with a breeding status were scarce. Furthermore, the simultaneous transversal study of age distribution and breeding status of the tagged females confirmed this trend of the demographic features exhibited by the female subantarctic fur seal population breeding at La Mare aux Elephants (Fig. 3).

The age at sexual maturity (ASM), defined as the period when individuals start to produce gametes (Bester 1995), can only be precisely determined by macroscopic and microscopic examinations of the gonads (Laws and Sinha 1993). However, this period is also underlined by a maximum age-specific growth, which is concurrent with the increasing pro-

Fig. 2. Age distribution frequency of breeding-age female subantarctic fur seals sampled during the 1999 breeding season ($n = 108$). Females tagged at birth are shown by the open histogram.

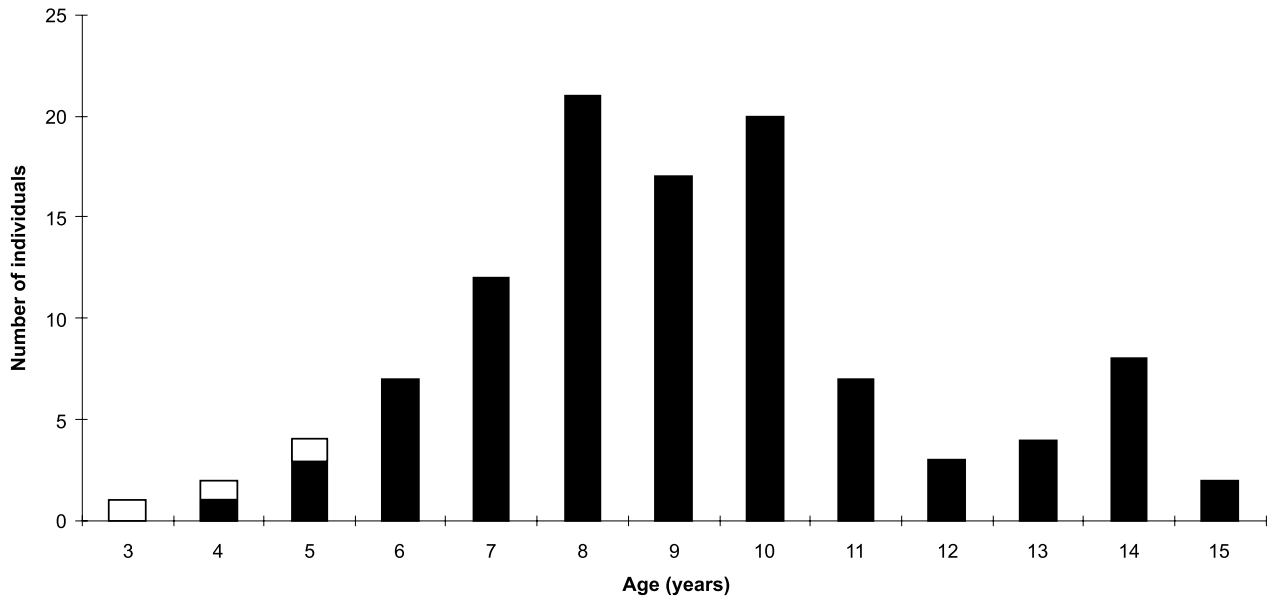
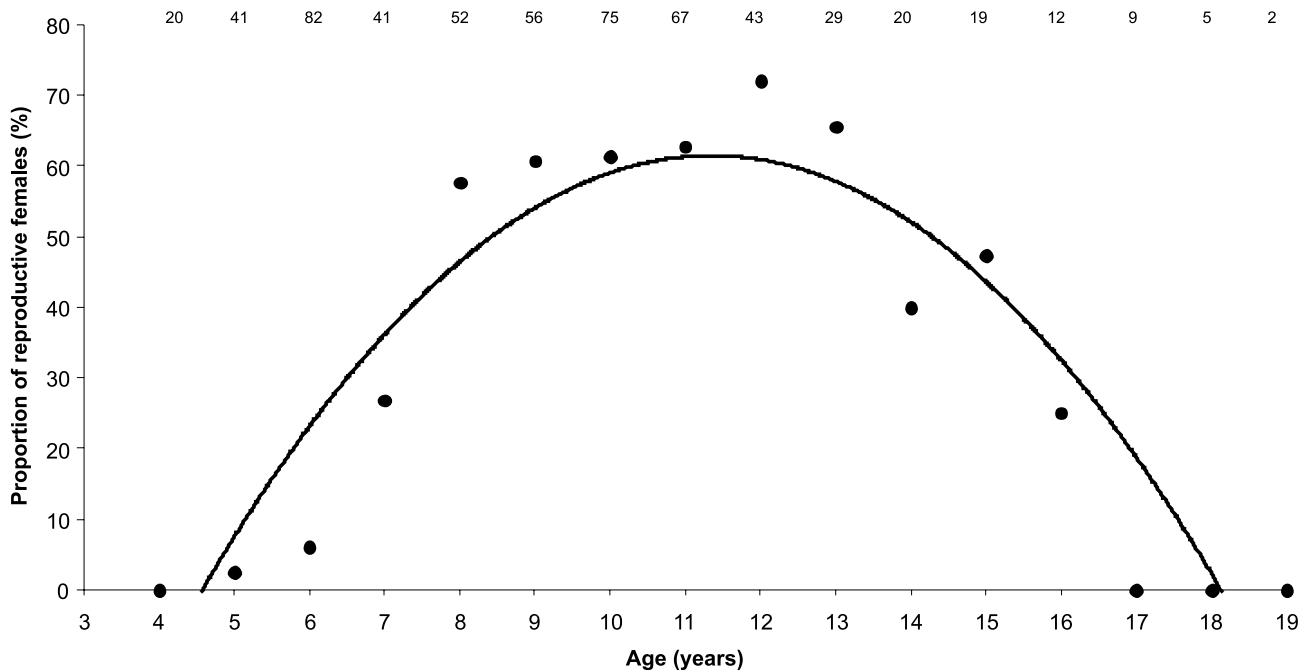


Fig. 3. Age-specific proportion of reproductive female subantarctic fur seals at Amsterdam Island obtained from the 1995–2003 transversal tag resightings. Sample sizes are shown at the top of the figure and the regression equation is $y = -1.338x^2 + 30.378x - 110.98$ ($r^2 = 0.85$).



portion of reproductive females observed in the 3- to 8-year-old age classes (Kingsley 1979; Berta and Sumich 1999). Laws (1956) found the body length at ASM to be remarkably constant among female pinnipeds at 87% of their final size, which would in this case correspond to a body length of 122.7 cm and be reached at 4 years of age (Fig. 1). The observed age at first reproduction (i.e., AFR = 5–6 years of age; Fig. 1) constituted the latest AFR ever recorded in a fur seal species (Wickens and York 1997), and thus, confirms a significant delay in the start of the process of sexual maturity. Accordingly, the body length at first reproduction was

127.6 cm, which is longer than that observed on the same species at first breeding on other southern islands (Table 1). Therefore, this delayed AFR suggests that the Amsterdam Island population experiences a lower rate of increase (see Stearns 1992) than do other subantarctic fur seal populations (Bester and Van Jaarsveld 1997). Moreover, this LAFR is consistent with a previous study on the same colony undergoing phase III of the recolonization process at that time (Roux 1987), which suggests a lack of influence of population density on this demographic parameter.

According to previous studies, the sexual maturation

phase is followed by a physical maturation phase (i.e., ossification processes and cartilaginous calcification), which cannot be observed on living animals (Bryden 1972; Perrin 1975). This phase occurs at the asymptotic length (AL = 141.0 cm) reached here for individuals older than 12 years of age. Hence, individual body length can only be used as an age estimate (Richards 1959; Hammill et al. 1995) when its length is below this limit. The adult female mean body length was 136.6 cm, which is similar to that found in a previous study on the same colony (Roux 1987), suggesting that AL was stable over time irrespective of population size. However, this mean body length is longer than that observed on the same species breeding on other southern islands (Table 1). Such large differences exclude discrepancies resulting from error introduced by fieldworkers, and thus, confirm the occurrence of a significant latitudinal graded difference in the size of adult female subantarctic fur seals (Bester and Van Jaarsveld 1994). This intraspecific variability in body length is in contrast with what has been found in most other southern hemisphere seal species (McLaren 1993). Although such differences between colony sites may be related to genotypic traits (Wynen et al. 2000), population density, or a combination of these factors (Bester and Van Jaarsveld 1994), this phenomenon may also be due to a lower per capita food availability that is indicative of an unstable prey abundance (Laws 1983; McLaren 1993; Bester and Van Jaarsveld 1997). This hypothesis is supported by the extreme foraging trip duration experienced by the females breeding on Amsterdam Island (Beauplet et al. 2004), and is also in accordance with the observed delay in the start of the sexual maturation phase, potentially leading to an allometric selectivity (i.e., the long distance between the rookery and foraging areas may lead to a positive selection for longer females, which are probably faster swimmers and are able to store a larger absolute amount of body reserves; Beauplet et al. 2004). Considering body reserves to be a decisive limiting factor when long foraging trip duration occurs also provides a good insight into the females' need to benefit from larger fat stores in order to have a successful reproductive event (Beauplet et al. 2004). This may explain the low mean reproductive rate ($R_{8-13} = 62.7\%$) observed in the most productive part of the breeding-age females' population compared with previous studies on the same and other southern fur seal species (Lunn et al. 1994; Bester 1995; Wickens and York 1997; Arnould et al. 2003); a significant part of this age-class group may experience temporary emigration (Fujiwara and Caswell 2002) and skip annual reproduction because of the energetic costs of maternal care (Costa and Gentry 1986; Oftedal et al. 1987; Clutton-Brock 1991) and because of environmental variations (Lunn et al. 1994; Boness and Bowen 1996; Trillmich 1996). Nevertheless, the reproductive rate of this population peaked in females from 8 to 13 years of age, which is consistent with the higher reproductive performances observed in other fur seal species of intermediate age (Lunn et al. 1994; Boltnev and York 2001; Arnould et al. 2003).

The mature cohort of older females declined after 13 years of age, which was represented by a sharp reduction in the number of individuals associated with a steadily decreasing proportion of breeding females (Fig. 3). Interestingly, females reproduced up to a maximum age of 16 years,

with no females older than 19 years of age observed in the population. This record is considerably lower than that previously found in the same (Bester 1995) and other fur seal species (Lunn et al. 1994; Boltnev and York 2001; Arnould et al. 2003). Considering that post-reproductive females were observed on the breeding colony (see Fig. 3) and the high site fidelity of this species (Gentry and Kooyman 1986; G. Beauplet, personal observation), it is very unlikely that any decline in visitation would reflect a switch in rookery, but rather a decline in survival after 13 years of age. Thus, this trend seems to highlight the evidence of a senescence effect (Promislow 1991) in this population of female subantarctic fur seals as previously hypothesized in other fur seal species (Trites 1991; Lunn et al. 1994; Boltnev and York 2001). In a previous study (Bester 1995), female subantarctic fur seals older than 13 years of age showed poor follicular development and the occurrence of some ovulation failure, suggesting that this population segment represented the cohort of older gradually post-reproductive females. Our results tend to suggest that this subantarctic fur seal population may combine the two strategies discussed in Boyd et al. (1995) whereby females start reproduction later, exhibit a low reproductive rate each year, but also die relatively young compared with other fur seals (Lunn et al. 1994; Bester 1995; Arnould et al. 2003; Dickie and Dawson 2003). The occurrence of senescence in wildlife populations may be determined by a diversity of regulatory agents of the population (Promislow 1991). The decreasing number of breeding females in older age classes may be related to low food availability, which also induces a delayed sexual maturity and a reduced reproductive rate. It is not clear, however, whether survival costs or reproductive state is the most important factor determining senescence (Boyd et al. 1995), but our study indicates that both factors are at work in the subantarctic fur seal population breeding on Amsterdam Island.

Conclusions

The population of female subantarctic fur seals breeding on Amsterdam Island exhibited a late start to reproduction, which was concurrent with the low survival of the older age classes. This consequently reduced the theoretical reproductive period for the population (i.e., from 5 to 16 years of age), which was also accentuated by the low reproductive rates experienced by all age classes (i.e., 5.2 reproductive events per individual throughout its reproductive life). Considering the mean pup preweaning survival rate calculated in a related study (Chambellant et al. 2003), this has led to a lower number of lifetime successfully weaned reproductive outputs per individual (i.e., 3.65 weaned pups per individual throughout its reproductive life). These results are consistent with low food availability and suggest that density-dependent regulatory processes are at work (Bester 1980). This hypothesis is confirmed by the decreasing preweaning growth rate performance in pups over the years at Amsterdam Island (Chambellant et al. 2003), probably in conjunction with the important population increase in the past years on Amsterdam Island (Bester 1987; Kerley 1987; Roux 1987). Such conditions may have led to a slowdown in the population increase (G. Beauplet and C. Guinet, unpublished data), which would influence demographic parameters (i.e.,

later age at first reproduction), and a faster turnover pattern of the most productive cohorts in the population.

Nevertheless, the limited information from transversal data (see Pistorius and Bester 2002) did not allow us to assess interindividual variability in lifetime reproductive success, age-specific survival, or individual reproductive frequency. Hence, a comprehensive longitudinal study of this population of known age will be presented in a separate paper. This separate paper will enable a more detailed analysis of population cohorts and their variations, which will facilitate further investigations of reproductive processes and maternal care that ultimately will allow for the assessment of population dynamics, fitness, and life history of this population of subantarctic fur seals throughout time.

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