Growth in pups of the subantarctic fur seal (*Arctocephalus tropicalis*) on Amsterdam Island

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Abstract

Growth in body mass in pups of the subantarctic fur seal *Arctocephalus tropicalis* was studied at Amsterdam Island, southern Indian Ocean during the rearing period between December 1995 and August 1996. We examined the change in the rates of mass gain and mass loss with pup age to explain the overall change in mass throughout the rearing period, when mothers alternate foraging trips at sea and attendance periods ashore. In the absence of their mothers, pups fast and lose mass. During the maternal attendance period ashore pups suck and gain mass. There was no significant difference in the rate of growth in mass between male and female pups. The rate of loss in mass during a fasting event was positively related to the initial body mass but negatively related to the age and duration of the fast of the pup. The rate of mass loss was best related to pup age by a quadratic relationship. The rate of mass loss increased until pups were 120 days old and then decreased until the end of the study period. The rate of gain in mass following a maternal foraging trip was positively related to the initial pup mass but negatively related to the foraging trip duration, and we found that the rate of mass gain decreased linearly with the age of the pup. The concomitant decrease in the rate of mass loss and mass gain for pups > 120 days old allowed pups to maintain a positive growth until they were 220 days old. After 220 days of age the rate of mass loss exceeded the rate of mass gain and the pups start to lose mass until weaning.

Key words: subantarctic fur seal, *Arctocephalus tropicalis*, pup growth, mass gain, mass loss

INTRODUCTION

In the subantarctic fur seal *Arctocephalus tropicalis*, pup rearing lasts 10 months, from December until mid-October (Tollu, 1974; Bester, 1981; Roux, 1986). During the pup rearing period, lactating females alternate foraging trips at sea and attendance periods ashore. At sea, the mother acquires the nutrients to cover her own energy expenditure and to gather sufficient reserves to produce milk for her pup. When the mother is at sea, the pup remains ashore and fasts until its mother returns and it can suckle.

Pup growth rate in mass results from the difference between the energy acquired by the pup when sucking and the energy lost when fasting on shore. The duration of the foraging trips of *A. tropicalis* females on Amsterdam Island is (with the Juan Fernandez fur seals *A. philippii*, Francis, Boness & Ochoa-Acuña, 1998) among the longest observed for any fur seal species studied. On Amsterdam Island, foraging trips last on

average 23 days in winter (Georges & Guinet, 2000). Despite the long foraging trips observed for *A. tropicalis* females at Amsterdam Island, their pups maintain a positive growth rate, but for the closely related Antarctic fur seal *A. gazella*, a foraging trip that exceeds 10 days results in massive mortality (Lunn & Boyd, 1993). The positive growth rate observed in *A. tropicalis* pups may result from either a higher level of energy acquisition by the pups relative to their mass, and/or a lower energy expenditure when fasting compared to the pups of other fur seal species. Most studies on pup growth in otariids have focused on overall mass change through the pup rearing period (Tollu, 1974; Crawley, 1975; Mattlin, 1981; Doidge, Croxall & Rickets, 1984; Kerley, 1985; Trillmich, 1986; Goldsworthy, 1995; Boltnev, York & Antonelis, 1998), some have estimated the mass gain (Georges & Guinet, 2000; Guinet, Goldsworthy & Robinson, 1999) or milk intake by pups consecutive to a foraging trip (Arnould, Boyd & Socha, 1996), but little attention has been paid on the way fasting pups lose mass. The growth rate of *A. tropicalis* pups at Marion Island was reported to decrease after 120 days of age until 203 days of age, and thereafter

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pups started to lose mass (Kerley, 1985). Data from Tollu (1974) on Amsterdam Island suggest that *A. tropicalis* pups reach their maximum mass at *c.* 225 days of age and then maintain their mass or start to lose mass. In a previous study Georges & Guinet (2000) found that serially weighed *A. tropicalis* pups at Amsterdam Island reached their maximum mass at 227 days of age.

We examined pup growth in mass during the rearing period of *A. tropicalis* pups at Amsterdam Island. The aim of this study was to determine the changes in the rate of mass gain, used as an index of the mother's food supply, and mass loss, used as an indicator of pup energy expenditure, through the pup rearing period and the consequences on the overall change in pup mass.

MATERIALS AND METHODS

Study site

The study colony was located at La Mare aux Elephants, north-east of Amsterdam Island (37°55′S, 77°30′E) in the southern Indian Ocean. Pups are born from late November to early January and weaning takes place between the end of September and late October. The mid departure date of the pups to sea is about mid-October, i.e. a 300-day nursing period (Tollu, 1974).

Tagging and weighing

Pups were individually identified by numbered plastic tags (Dalton Rototags, Dalton supply, Nettlebed, U.K.) placed on the trailing edge of the fore flipper (see previous paper).

From birth, in December 1995, until the end of August 1996 the study colony was checked daily and all tagged pups found in the colony were weighed on spring scales (20 ± 0.1 kg and 25 ± 0.1 kg). The maternal attendance pattern was based on the daily monitoring of changes in pup mass. The fast duration (foraging trip of the mother) was considered to start from the first day pups lost mass until the first day they gained mass when the female returned (Fig. 1) while the sucking period (the attendance period of the mother) was considered to start on the day pups gained mass and stopped on the first day pups lost mass (Fig. 1). This method was validated in 1995 using small VHF radio transmitters glued to the fur of lactating females. No differences were found between the maternal attendance calculated from pup mass changes and from monitoring of presence-absence ashore using VHF transmitters (Georges & Guinet, 2000).

We defined a foraging cycle as the sum of the fast duration (FD) of the pup (i.e. the foraging trip duration (FTD) of the mother) and the sucking period duration (S) of the pup (i.e. the shore bout duration (SBD) of the mother; Fig. 1).
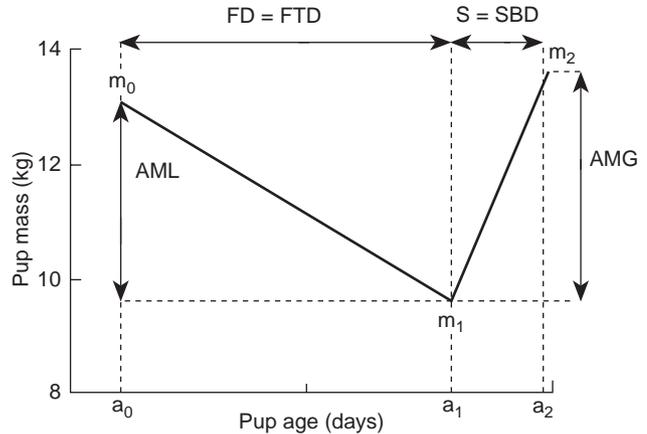
All the mass units are given in kilograms and the time

Fig. 1. A schematic of pup mass change throughout a foraging cycle: with initial mass (m_0) and initial age (a_0) of the pup at the end of the first shore bout, mass (m_1) and age (a_1) of the pup at the end of the fast duration (FD) and mass (m_2) and age (a_2) of the pup at the end of the second sucking period duration (S). AML, absolute mass loss; AMG, absolute mass gain. The fast duration (FD) of the pup is equivalent to the foraging trip duration (FTD) of its mother and the sucking period (S) is equivalent to the shore bout duration (SBD) of the mother.

units are in days. The absolute mass loss (AML) was determined as the difference between the maximum mass or initial mass (m_0) at the end of a sucking period (S), and (m_1) the mass at the beginning of the next feeding event. Absolute mass gain (AMG) was calculated as the difference of mass of the pup at arrival of the mother (m_1) at the end of the fast duration and the maximum mass (m_2) at its departure at the end of the sucking period. During the whole pup rearing period, AMG and AML were monitored for 123 different pups for 991 foraging cycles (FC) (mean = 8.1 FC, SE = 3.4, range 1–17 FC). One AML and the consecutive AML measured over the same foraging cycle were randomly selected for each of the 123 pups to respect the independency criteria for the analysis. Analyses were all conducted using this independent data set. AMG and AML could not be averaged for each pup for the different foraging cycles as these parameters are related to pup mass and pup age which are changing through the pup rearing period. The age of the pup at the beginning of a foraging cycle ranged from 13 to 250 days for this data set.

The rate of mass loss in kg.day^{-1} was calculated as the AML divided by FD while the rate of mass gain kg.day^{-1} was calculated as the AMG divided by FTD (or FD) which indicated the mass gained by the pup relative to the duration of the FTD of the mother. The rate of net mass gain (RNMG) in kg.day^{-1} was calculated as the difference between the AMG and AML of the pup divided by the foraging cycle duration (FD + the consecutive SBD)

$$\text{i.e. RNMG} = [(m_2 - m_1) - (m_0 - m_1)]/$$
$$(FD + SBD) = (m_2 - m_0)/FD.$$

As the mass of the pup varied widely over a foraging cycle, we calculated the mid-sucking mass and mid-sucking age for each pup. The mid-sucking mass in kilograms being defined as:

$$(m_1 + m_2)/2$$

and the mid-sucking age in days:

$$(a_1 + a_2)/2.$$

The mass-specific rate of mass loss in per cent per day was calculated according to the following relationship:

$$(\ln(m_1) - \ln(m_0))/FD \times 100$$

Relationships between factors were analysed using general linear model (GLM) when multivariate analyses were used. Tables only include the contribution of significant factors to the model, and slopes correspond to the model after stepwise backward analysis (level of significance $P < 0.1$). Analyses were performed using the SYSTAT statistical packages (SYSTAT, 7.0 statistics, SPSS Inc., U.S.A.) and statistical significance was considered to be $P < 0.05$.

RESULTS

Foraging trip and shore bout duration

Foraging trip duration and thus fast duration of the pups was not related to the sex of the pup ($F_{1, 121} = 1.73$, $P = 0.19$) but was significantly related to pup age ($F_{1, 121} = 147.50$, $P < 0.001$, Fig. 2) and to the mass of the pup ($F_{1, 121} = 25.45$, $P < 0.001$) with:

$$FTD = 12.871 - 1.278\,mass + 0.141\,age$$
$$(r^2 = 0.64, n = 123, P < 0.001).$$

Fig. 2. Relationship between foraging trip duration (FTD) and pup age for *Arctocephalus tropicalis* at Amsterdam Island by the linear equation: $FTD = 4.597 + 0.094\,age$ ($r^2 = 0.566$, $n = 123$, $P < 0.001$).

The shore bout duration in days (mean = 3.6, $SE = 1.6$, $n = 123$) was not related to any of the parameters studied: sex ($F_{1,121} = 0.03$, $P = 0.86$), pup age ($F_{1,121} = 0.19$, $P = 0.73$) and pup mass ($F_{1,121} = 0.116$, $P = 0.75$).

Mass change according to pup age

The mid-sucking mass of the pup was not related to the sex ($F_{1,121} = 0.45$, NS), but was linearly related to the mid-sucking age of the pup (mass = $4.830 + 0.045\,age$, $r^2 = 0.60$, $n = 123$, $P < 0.001$) but the best relationship was found using the quadratic equation:

$$mass = 4.8301 + 0.0660\,age - 0.0001\,age^2$$
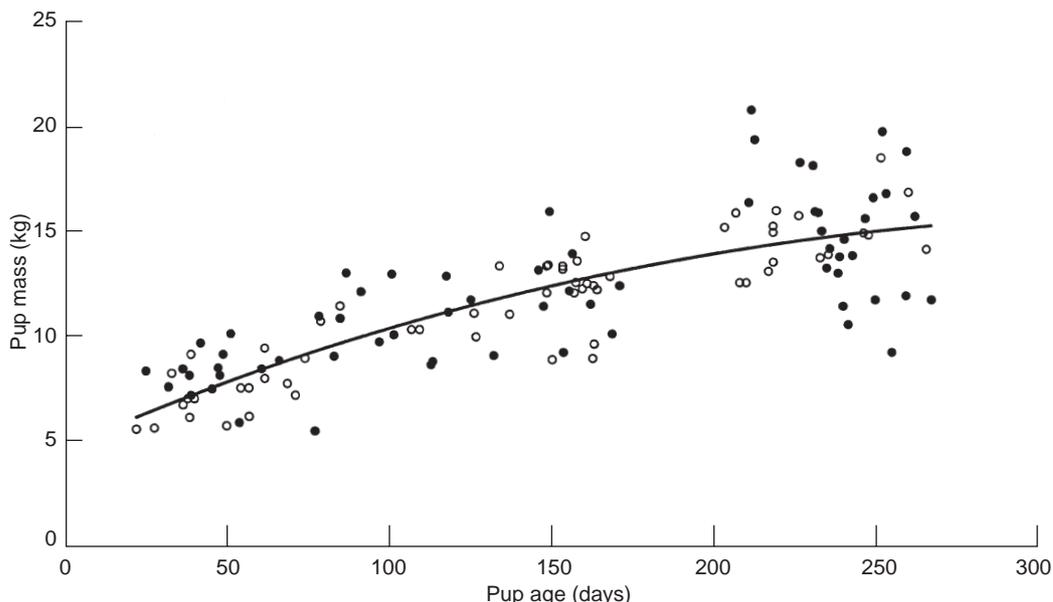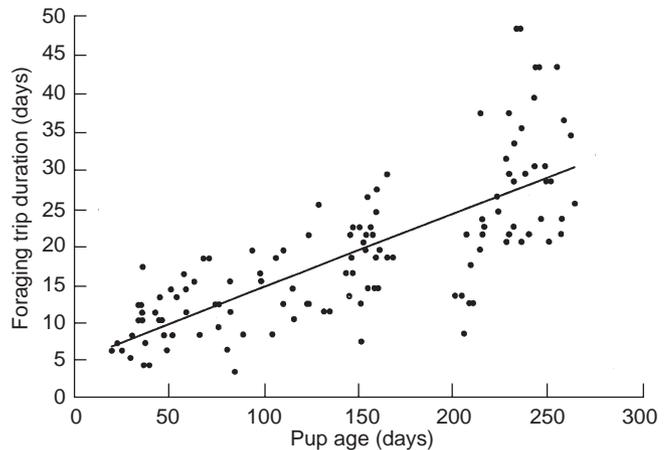$$(r^2 = 0.66, n = 123, P < 0.001) \text{ (Fig. 3)}$$

Fig. 3. Change in mass (mid-sucking mass) for male (●) and female (○) *Arctocephalus tropicalis* pups according to their age (mid-sucking age: see text for details) at Amsterdam Island. Pup mass was best related to pup age according to the quadratic equation: mass = $0.483 + 0.066\,age - 0.0001\,age^2$ ($r^2 = 0.66$, $n = 123$, $P < 0.001$).

Table 1. Mass gain parameters according to pup sex, pup age, pup mass and foraging trip duration

| Dependent variables	r^2	Model P	n	Pup sex		Pup age (days)	Pup mass (kg)	Foraging trip duration (days)	Constant
							Independent variables		
Absolute mass gain (kg)	0.372	<0.001	123	NS	t	−6.375	6.988	6.508	0.812
					Coefficient	−0.018	0.313	0.094	0.299
				$P = 0.550$	P	<0.001	<0.001	<0.001	0.419
Rate of mass gain (kg/day at sea)	0.638	<0.001	123	NS	t	−7.214	7.111	−2.502	7.68
					Coefficient	−0.001	0.022	−0.002	0.195
				$P = 0.278$	P	<0.001	<0.001	0.014	<0.001
Rate of net mass gain (kg/day at sea)	0.334	<0.001	123	NS	t	−3.267	2.341	−1.702	2.853
					Coefficient	−0.0004	0.005	−0.002	0.054
				$P = 0.11$	P	<0.001	0.021	0.091	0.005
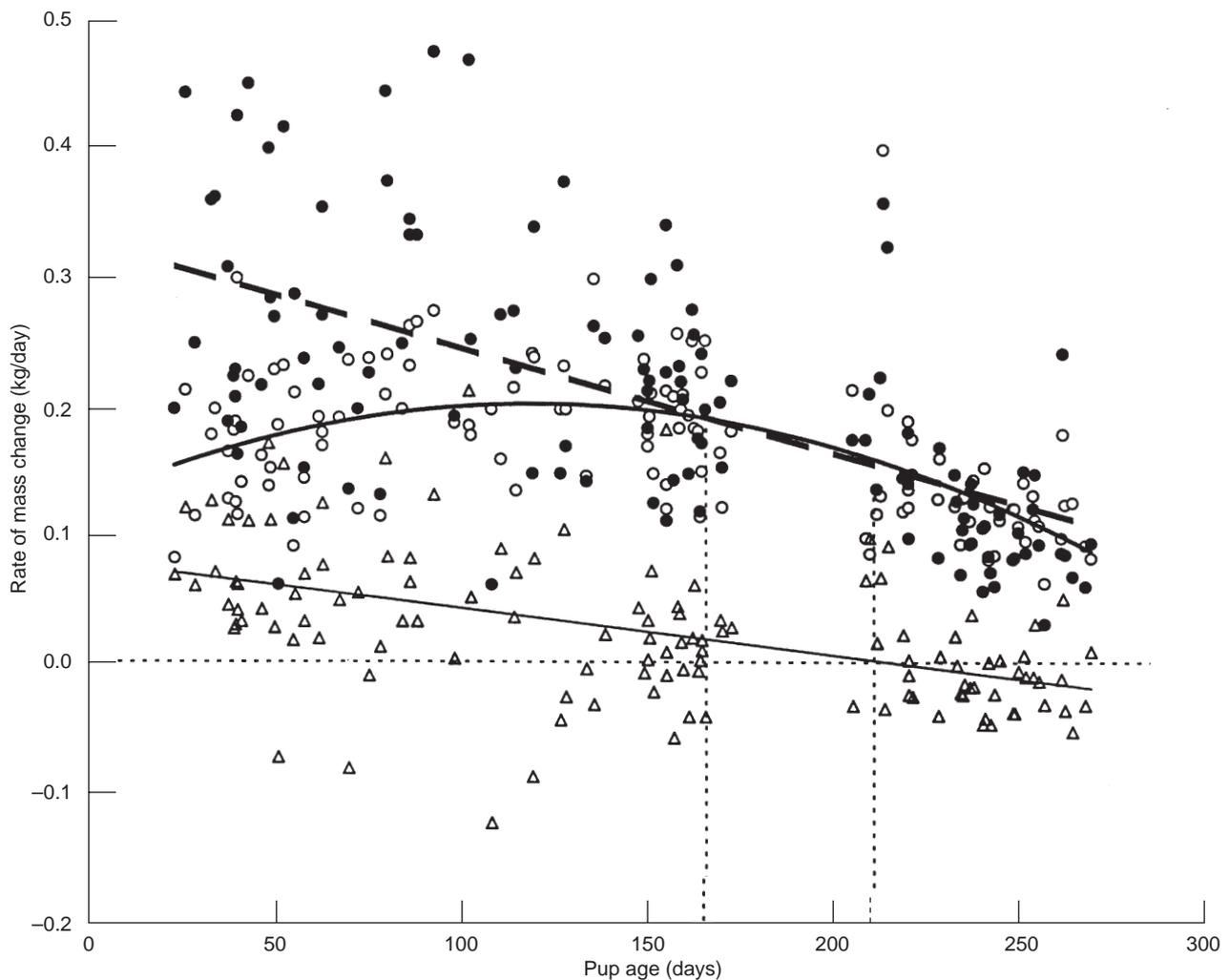
Fig. 4. Relationship between pup age and the rate of mass gain (● and dashed bold line: RMG = 0.326 − 0.0008age, $r^2 = 0.37$, $n = 123$, $P < 0.001$); rate of mass loss (○ and bold line: RML = 0.1329 + 0.0012age − 0.00005age^2, $r^2 = 0.33$, $n = 123$, $P < 0.001$), and rate of net mass gain (△ and thin line: RNMG = 0.0796 + 0.0004age, $r^2 = 0.24$, $n = 123$, $P < 0.001$). Horizontal thin dashed line, a nul rate of mass change; first vertical dashed line to the left, age (165 days) at which the RMG just compensates for the RML; second vertical dashed line, age (220 days) at which the RML starts to exceed the RMG which results in a negative RNMG.

Table 2. Mass loss parameters according to pup sex, pup age, pup mass and foraging trip duration

Dependent variables	Model r^2	P	n	Pup sex		Pup age (days)	Pup mass (kg)	Fast duration (days)	Constant
Absolute mass loss (kg)	0.779	< 0.001	123	NS	t	− 8.570	11.131	12.918	− 4.053
					Coefficient	− 0.014	0.284	0.100	− 0.879
				$P = 0.136$	P	< 0.001	< 0.001	< 0.001	< 0.001
Rate of mass loss (kg/day at fast)	0.595	< 0.001	123	NS	t	− 8.248	10.306	− 5.092	6.317
					Coefficient	− 0.001	0.016	− 0.002	0.111
				$P = 0.984$	P	< 0.001	< 0.001	< 0.001	< 0.001
Mass specific rate of mass loss (%)	0.341	< 0.001	123	NS	t	− 11.451	2.683	− 3.865	24.548
					Coefficient	− 0.009	0.033	− 0.014	2.566
				$P = 0.822$	P	< 0.001	0.001	0.001	< 0.005

Mass gain of the pup

The age and mass of the pup used for this analysis are the age and mass at the beginning of the shore bout of the mother (a_1 and m_1; Fig. 1). The sex of the pup had no effect on any of the parameters of mass gain studied. Absolute mass gain (AMG) decreased significantly with the age of the pup but increased significantly with duration of the foraging trip and pup mass (Table 1). The rate of mass gain (RMG) decreased with increasing foraging trip duration and pup age but increased with pup mass (Table 1). RMG was related to pup age by the linear equation:

$$RMG = 0.326 - 0.0008\,age \ (r^2 = 0.37, n = 123, P < 0.001)$$
(Fig. 4).

The rate of net mass gain (RNMG) was negatively related to pup age but positively related to pup mass. The RNMG tended to be negatively related to the foraging trip duration (Table 1). The RNMG was related to pup age by the linear equation:

$$RNMG = 0.0796 - 0.0004\,age \ (r^2 = 0.24, n = 123, P < 0.001)$$

Mass loss of the pup

The age and mass of the pup taken into account in this analysis correspond to the age and the mass of the pup at the beginning of the fasting event (a_0 and m_0; Fig. 1). The sex of the pup had no effect on any of the parameters studied (Table 2). Absolute mass loss during a fasting event increased with the initial mass of the pup and fast duration, but decreased with increasing pup age (Table 2).

The rate of mass loss (RML) of the pup increased significantly with the initial mass of the pup but was negatively related to the fast duration and the age of the pup (Table 2). The rate of mass loss was significantly related to pup age by the linear equation ($RML = 0.211 - 0.003\,age$, $r^2 = 0.13$, $n = 123$, $P < 0.001$) but the best relationship was found using the quadratic equation:
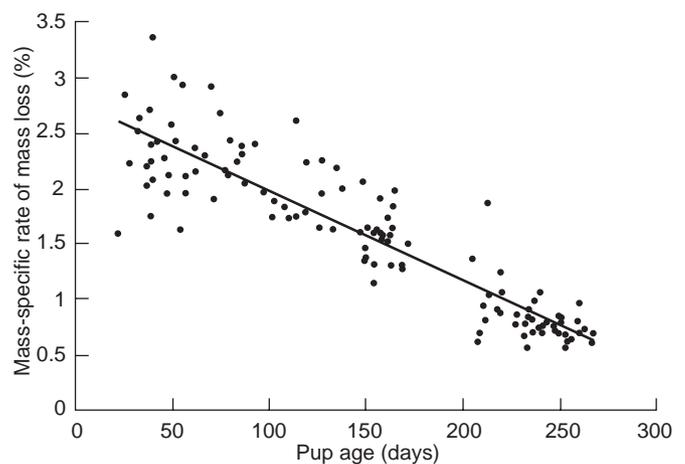
$$RML = 0.1329 + 0.0012\,age - 0.00005\,age^2$$

Fig. 5. Relationship between the mass-specific rate of mass loss and pup age for *Arctocephalus tropicalis* at Amsterdam Island: $MSRML = 2.7759 - 0.0079\,age$, ($r^2 = 0.81$, $n = 123$, $P < 0.001$).

$$(r^2 = 0.33, n = 123, P < 0.001) \text{ (Fig. 4)}.$$

The mass-specific rate of mass loss (MSRML) decreased both with the age and fast duration but was found to increase with the initial mass of the pup (Table 2). The MSRML was best related to pup age using the linear equation:

$$MSRML = 2.776 - 0.008\,age \quad (r^2 = 0.81, \quad n = 123, \ P < 0.001) \text{ (Fig. 5)}.$$

DISCUSSION

The growth rates of *A. tropicalis* pups up to weaning (i.e. 45 g/day) in our study are of the same order as those previously at Amsterdam Island (Tollu, 1974) and Marion Island (Kerley, 1985). In this study *A. tropicalis* pups of a given mass were gaining and losing mass at the same rate regardless of their sex which resulted in an identical growth rate from birth until 250 days of age. Sex differences in pup growth rate were found on *A. tropicalis* pups in previous studies both on Amsterdam Island (in Kerley, 1985 from Tollu, 1974)

and on Marion Island (Kerley, 1985) with male pups growing faster than female pups. One possible explanation for the absence of sex differences in pup growth rate in our study compared to those obtained by Kerley (1985) is the assumption made by Kerley, as a result of a limited sample size, that male and female pups had the same birth mass. However, several studies indicate that at birth, *A. tropicalis* male pups are heavier than female pups (Roux, 1986; Bester & Van Jaarsveld, 1994; see previous paper) and this is consistent with the results of previous work on other otariid species (*A. gazella*, Payne, 1979; Doidge *et al.*, 1984; *Callorhinus ursinus*, Trites, 1993; *A. galapagoensis*, Trillmich, 1986). The assumption of a similar birth mass between male and female pups made by Kerley (1985) leads to an underestimation of the pup growth of the female pups and an overestimation of male pup growth rate, and thus may lead to significant differences in pup growth rates between sexes. Significant differences were found using cross-sectional data between sexes on *A. gazella* (Doidge *et al.*, 1984), *A. galapagoensis* (Trillmich, 1986), *A. pusillus* (Rand, 1956; Mison-Jooste, 1999) with male pups growing more rapidly than female pups. Serially weighed male *A. gazella* pups were found to grow significantly faster than female pups (Goldsworthy, 1995; Guinet, *et al.*, 2000). Interestingly in one of these studies, the difference in growth rate between male and female pups was related to a higher rate of mass loss in female pups compared to male pups while no sex differences were found in the rate of mass gain (Guinet *et al.*, 2000). However no significant differences were found in *A. gazella* using serial data (Lunn *et al.*, 1993; Lunn & Arnould, 1997). These contrasted results on sex differences in pup growth are difficult to interpret, and in a review on maternal investment in pinnipeds Trillmich (1996) suggested that the absence or presence of sex differences in pup growth may vary according to environmental factors, such as the availability of prey.

Pup growth rate results from the difference of the resources acquired by the pup when sucking and the resources expended by the pup over the rearing period. Growth should stop when the maternal resources transferred to the pup just compensate for pup energy expenditure. Although it seems obvious that pup growth rate in mass should be directly related to the level of maternal input into her pup (i.e. we found that heavier pups were gaining more mass than smaller pups for a given age and foraging trip duration), this study shows that the growth in mass of *A. tropicalis* pups is achieved by the concomitant change in the rate of mass gain and the rate mass loss of the pup (Fig. 4). The rate of mass gain decreased throughout the whole pup rearing period from about 300 g/day at the beginning of the pup rearing period to < 150 g/day when pups were 250 days old at the end of the study period, which corresponds to the austral winter when food availability is lower. The food availability hypothesis seems to be confirmed by our previous finding (Georges & Guinet, 2000) indicating that mothers were unable to maintain their milk delivery rate to their pups in winter compared to summer despite increased diving effort.

The rate of mass loss tended to increase throughout the first part of the pup rearing period and reached its maximum rate when pups were about 120 days old and then decreased until the end of the study period. The decrease of the rate of mass loss through the second part of the rearing period allowed the pups to compensate for the decreasing rate of mass gain. According to Fig. 4 the rate of mass gain just compensates for the rate of mass loss between 165 days and 220 days of age, and no pup growth was observed for pups older than 165 days ($r^2 = 0.015$, $n = 45$, NS). For pups older than 220 days the rate of mass loss exceeded the rate of mass gain, indicating that the pups were starting to lose mass. This finding is consistent with a maximum *A. tropicalis* pup mass at Amsterdam Island found at 225 days of age in 1973 in cross-sectionally sampled pups (Tollu, 1974) and 227 days of age in serially weighed pups (Georges & Guinet, 2000). Kerley (1985) measured the maximum mass of *A. tropicalis* pups at Marion Island at 203 days of age. This is slightly earlier than found in our study, but is encompassed by the 165–220 days of age period for which no significant pup growth was observed in our study. The difference observed between this study and Kerley (1985) can also be explained by methodological differences. The age of maximum mass given by Kerley (1985) corresponds to the maximum mean mass value observed for pups weighed on 13 occasions through the pup rearing period, but no measurements of mass were done between 203 and 251 days of age.

For pups older than 150 days the decrease in the rate of mass loss (Fig. 4) despite increasing pup mass (Fig. 3) is achieved by the decrease of the mass-specific rate of mass loss with increasing age (Fig. 5, Table 2) and foraging trip duration (Fig. 2, Table 2). This negative relationship between the mass-specific rate of mass loss and age could be the result of the lower metabolic needs per unit of mass of larger bodies (Kleiber, 1961; Schmidt-Nielsen, 1983; Schmitz & Lavigne, 1984). Baker, Fowler & Antonelis (1994) reported that the rate of mass loss was unrelated to the initial mass among immature male northern fur seals, but reported a decrease in the rate of mass loss when comparing juveniles and adult males. No differences were found in the mass-specific rate of mass loss in relation to the mass in *A. gazella* pups (Arnould *et al.*, 1996; Guinet *et al.*, 2000) or fasting adult males (Boyd & Duck, 1991).

The decrease in the mass-specific rate of mass loss according to the age of the *A. tropicalis* pups should be further investigated and may reflect better thermoregulation as a result of a change in body composition and in the properties of the fur. The insulation of the fur was likely to be improved, in particular when swimming in water, after the moult occurred in March–April for *A. tropicalis* (pers. obs.). Furthermore, the decrease in the mass-specific rate of mass loss with an increasing fast duration for a given age and a given mass suggests that pups adjust their activity, and thus their energy

expenditure, with the depletion of fat stores associated with a prolonged fast, as observed on Amsterdam Island. We found that when age and fast duration are taken into account, the mass-specific rate of mass loss increased with pup mass. This result suggests that pups that are growing faster in mass have a higher expenditure than slow-growing pups.

This work suggests that there is no evidence of differences in pup growth rate in mass and pup maximum mass between our study and the study conducted in 1973 by Tollu (1974) at Amsterdam Island. Records indicate that the population was increasing rapidly when Tollu's study took place (Roux, 1987) but was likely to be stable in 1996 (Guinet, Jouventin & Georges, 1994), suggesting that the population had probably reached the carrying capacity of the environment. Consequently we should have expected a lower pup growth rate in 1996 compared to 1973. However, large inter-annual differences in pup growth rate are observed in other fur seal species (*A. gazella*, Lunn & Boyd, 1993; *A. pusillus*, Mison-Jooste, 1999) indicating that comparison of pup growth performances between only 2 years has no significance to detect any trends.

Although most of the studies have compared species in terms of overall growth rate, this study establishes how the balance between the rate of mass gain and mass loss varies with pup age and determines the mass growth of *A. tropicalis* pups at Amsterdam Island. We suggest that future studies on pup growth should investigate the relative importance of the rate of mass gain (energy acquisition) or mass loss (energy expenditure) on mass growth rate. This may help us to understand if the differences in pup growth rate between species, but also within species, result from differences in rate of mass gain, rate of mass loss, or the combination of both factors.

Acknowledgements

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