

# Differential resource allocation strategies in juvenile elephant seals in the highly seasonal Southern Ocean

Iain C. Field<sup>1,2,3,\*</sup>, Corey J. A. Bradshaw<sup>1,3</sup>, Harry R. Burton<sup>2</sup>, Mark A. Hindell<sup>1</sup>

<sup>1</sup>Antarctic Wildlife Research Unit, School of Zoology, University of Tasmania, Private Bag 05, Hobart, Tasmania 7001, Australia

<sup>2</sup>Australian Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia

<sup>3</sup>School for Environmental Research, Charles Darwin University, Darwin, Northern Territory 0909, Australia

**ABSTRACT:** Environmental conditions experienced in early life affect growth and influence life history strategies, especially in seasonal environments. We studied the seasonal and sexual variation in resource allocation in juvenile southern elephant seals to investigate whether they show a seasonal decline in growth. We also examined whether sexual differences in growth may lead to separate growth strategies that suit each sex in maximizing fitness. We examined the variation in length (as a measure of somatic growth), body mass and condition of 470 individual 1- to 4-yr-old elephant seals relative to their different growth strategies. Applying a novel growth function, we observed increased somatic growth in summer compared to winter. Males were larger, had higher proportions of lean tissue and grew faster than females, demonstrating the evolution of a male growth strategy of attaining maximum size quickly, and a female strategy of achieving primiparity at an early age. This evidence supports the idea that seasonal patterns reflect seasonal variation in prey availability and quality, and differential growth strategies promote optimal resource allocation and increase an individual's probability of survival and future breeding success in the highly dynamic and seasonal Southern Ocean.

**KEY WORDS:** Southern elephant seals · Resource allocation · Growth · Sexual dimorphism · Seasonal environment

—Resale or republication not permitted without written consent of the publisher—

## INTRODUCTION

Quantifying somatic growth and variation in body-mass is a fundamental component of understanding the life history of a species (Peters 1983). How rapidly an individual progresses from juvenile to adult status is a trade-off between allocation of resources for somatic growth versus development of reproductive potential (Stearns 1992). In other words, an individual can spend more time growing to a larger size, or it can divert resources to reproduction or preparation for reproduction and sacrifice achieving larger body mass quickly. The resolution of this trade-off is particularly important where food availability and energy use limit survival and reproductive output (Boyce 1985). Juvenile growth, regarded here as changes in body mass or length with age, can be an important element affecting

survival (Lindström 1999, Hall et al. 2001, McMahon et al. 2003), reproductive performance and, ultimately, rates of population change (Sand 1996, Boyd 2000, Post & Parkinson 2001).

Growth can be influenced by both intrinsic (age, sex and developmental physiology) and extrinsic (seasonal and annual environmental variation, and changes in food availability and quality) factors (Caughley & Sinclair 1994). For example, seasonal growth can affect reproduction and survival for many species (Lindström 1999), although previous studies have focused mainly on small predators or long-lived herbivores. Such studies are difficult with large free-ranging predators, due to the need for long-term data, along with high frequency of captures within annual cycles and across extreme environmental gradients (Caughley & Sinclair 1994).

\*Email: iain.field@cdu.edu.au

The Southern Ocean is a highly dynamic environment that has broad- and fine-scale spatio-temporal fluctuations in various physical properties of the regional water masses (Rintoul et al. 1997) and sea ice cover (Arrigo et al. 1998) that influence the diversity, distribution and abundance of the biological communities (Rodhouse & White 1995, Arrigo et al. 1998). The southern elephant seal *Mirounga leonina* is an apex predator in the Southern Ocean (Bradshaw et al. 2003). Due to its haul-out patterns and availability for capture, it is an excellent model species for studying intrinsic and extrinsic influences determining juvenile growth strategies in an extremely seasonal environment.

Juvenile southern elephant seals have a distinct annual cycle that is strongly influenced by the selective pressures of resource limitation and intra-specific competition (Field et al. 2005a). The species is highly size-dimorphic and polygynous, with mature males that may be 8 to 10 times heavier than females. To achieve this superlative dimorphism, the sexes have vastly different growth rates during the juvenile and sub-adult stages. Initially however, male and female seals grow at similar rates, with females exhibiting a conventional mammalian growth curve with a reduction of growth rate toward puberty (Bell et al. 2005). However, male growth accelerates exponentially after 4 yr of age until maximum body size is reached at approximately 10 yr (McLaren 1993 and references therein).

For southern elephant seals, population status and rate of population change are mediated mostly by food resource availability (McMahon et al. 2005 and references therein). The food supply effect may be observed in growth-related factors such as changes in age at primiparity, fecundity and survival. The survival of juvenile (1 to 3 yr) southern elephant seals is the most important factor influencing the rate of change in the declining elephant seal population at Macquarie Island (McMahon et al. 2003). As it progresses from juvenile stages toward maturity, an individual's growth rate, and ultimately, its adult body size, may be influenced by ontogenetic changes in morphology and physiology, due to the selective pressures driving sexual dimorphism, metabolic requirements, foraging behaviours that reduce intra-specific competition, the availability of prey, or a combination of these factors (Hindell et al. 1994, Field et al. 2005a,b). Therefore, it is hypothesized that the sensitivity of juveniles to variation in environmental conditions results from their higher energetic requirement for growth, lack of foraging experience and the need to adjust behaviour in response to continuous morphological, physiological and hormonal changes (Brafeld & Llewellyn 1982).

Several functions have been used to describe the growth of pinnipeds (reviewed in McLaren 1993); however, in the past all of these functions have been based

on relatively small samples and have assumed that growth is constant throughout the year. Recent studies of other marine vertebrates, including fish and other seal species, have demonstrated a seasonal component to growth and have hence modified traditional growth curves to incorporate this seasonal variation (Beck et al. 2003, Eveson et al. 2004). Until now, the combined effects of intrinsic and extrinsic factors on juvenile growth, particularly in long-lived species, have been unclear. In this study we describe annual and seasonal growth in length, mass and the associated changes in body composition of southern elephant seals between the ages of 1 and 4 yr. We predict that (1) rates of gain for lean and blubber masses during summer and winter and (2) seasonal variation in resource patterns influence male and female growth trajectories differently, resulting in a divergence in growth toward earlier development and age of primiparity in females and large size in males. We then discuss these trends in light of the selective pressures associated with living in this highly challenging and variable Southern Ocean environment in which southern elephant seals spend more than 80 % of their life cycle.

## MATERIALS AND METHODS

Individual juvenile southern elephant seals ( $n = 470$ ) of known age marked at either birth or weaning were captured between November 1999 and February 2001 as part of a long-term demographic study of the population on Macquarie Island (McMahon et al. 2003). Some seals ( $n = 104$ ) were also caught consecutively at the start of concurrent haul-outs, providing a smaller longitudinal dataset. Seals were caught and immobilized as they returned for their moult and mid-year haul-outs. Seals ranged in age from 13 to 46 mo at the time of capture and were subsequently allocated into 1-, 2- and 3-yr-old age groups and into moult and mid-year or 'winter' haul-out categories. We assumed that the data collected at the start of the moult haul-out (November to December) would reflect austral winter foraging and associated growth, whereas data from the start of the mid-year haul-out (March to June) would be associated with summer foraging and growth.

Seals were caught by placing canvas bags over their heads (McMahon et al. 2000) and physically restraining them until prescribed doses of a 1:1 mixture of tiletamine and zolazepam (Telazol<sup>®</sup>, Forte Dodge) were administered intravenously (Field et al. 2002). Once immobilized, seals were weighed using a digital scale ( $\pm 1$  kg), and snout-tail lengths (STL;  $\pm 1$  cm) were measured (Field et al. 2002). All data presented in the text or tables are shown as  $\bar{x} \pm SD$ , and those in the figures as  $\bar{x} \pm 2 \times SE$ .

**Blubber mass as a percentage of body mass (body composition).** For 211 of the captured individuals (45%), serial lengths, girths and ultrasound measurements of blubber depth were made to calculate body composition (Gales & Burton 1987, Field et al. 2002). These morphometric measurements were made across 7 sections, with the head and hips to the base of the tail forming cones and the rest of the body sections forming truncated cones (Field et al. 2002). Measures of blubber thickness corresponding with the girth measurements along the seal's dorsal side were obtained using an ultrasound backfat depth system (A-Scan Plus™, Sis-Pro). This method assumes that all lipid energy reserves are stored in the blubber, which lies in the hypodermis over the whole body, except for the flippers that contain insignificant amounts of subcutaneous fat (Slip et al. 1992, Field et al. 2002). From these morphometric and ultrasonic measurements, total blubber and lean (or 'blubber-free') tissue volumes were calculated, and from these we estimated body composition expressed as the percentage of blubber by mass. This method also assumes that individuals are circular in cross-section. Total blubber mass (Slip et al. 1992, Webb et al. 1998) was calculated by multiplying blubber volume by its density, taken as 0.95 g cm<sup>-3</sup> (Gales & Burton 1987). This technique has been validated with isotopic techniques in the calculation of body composition (Webb et al. 1998) and real measurements of blubber depth using a steel ruler (Mellish et al. 2004), with a mean error of 0.01 ± 4.25%. Lean body mass was calculated by subtracting the blubber mass from the total body mass. Hereafter, we define blubber mass as fat mass, and lean or 'blubber-free' tissue as lean mass. Body composition is defined as fat mass as a percentage of total body mass.

**Modelling rates of mass gain.** To describe the general patterns of net mass, lean mass and fat mass gain while the seals were at sea, we used the mean arrival body mass and composition values from this study, and the mean haul-out duration, mass loss rate and body composition at the end haul-out for each sex and age group during the moult and mid-year haul-outs described in Field et al. (2005b) and in unpublished data for 3-yr-old males and females (Table 1).

**Seasonal growth.** Because elephant seals are highly size dimorphic, we modelled the growth of males and females separately. We used a maximum likelihood approach, fitting a von Bertalanffy (vB; McLaren 1993) growth function (Eq. 1) to individual STL (*L*) and age in days (*a*) of the form:

$$L = L_{\infty}(1 - e^{-k(a-a_0)}) \quad (1)$$

where *k* and *a*<sub>0</sub> (the theoretical age at which length is 0) are constants. Female asymptotic lengths (*L*<sub>∞</sub>) were assumed to be 2.57 m (Bell et al. 2005) and 3.11 m for

Table 1. *Mirounga leonina*. Snout-tail length (STL), body mass and condition ( $\bar{x} \pm SD$ ) of 1-, 2- and 3-yr-old southern elephant seals measured at the start of the moult and mid-year haul-outs. Also shown are the duration, proportion of mass loss and end body condition (from Field et al. [2005b, and unpubl. data] for 3-yr-old southern elephant seals; denoted by \*) used in the calculation of lean and fat masses at the start and end of a haul-out, and the number of individuals used to calculate the body composition (nbc) at the start of a haul-out

Age	Haul-out	n (nbc)	Age (days)	Haul-out duration (days)*	STL (m)	Body mass (kg)	Body composition (% fat)	Mass loss (%)*	End Body mass (kg)	End Body condition (% fat)*	Lean mass (kg)	End lean mass (kg)	Fat mass (kg)	End fat mass (kg)
<b>Female</b>	1	47 (13)	418.34 ± 15.04	31.75	1.67 ± 0.09	165.77 ± 24.12	26.15 ± 3.60	31.68	113.25	16.92	122.42	94.09	43.35	19.16
		50 (33)	559.06 ± 55.17	22.75	1.80 ± 0.11	198.50 ± 24.55	30.31 ± 2.59	18.53	161.72	23.97	138.33	122.95	60.17	38.76
	2	45 (10)	772.24 ± 8.59	32	1.86 ± 0.12	235.29 ± 35.49	27.82 ± 2.26	34.23	154.75	17.70	169.82	127.36	65.47	27.39
		29 (23)	937.69 ± 32.40	22.88	2.03 ± 0.13	290.52 ± 36.38	30.30 ± 1.76	15.71	244.88	26.31	202.48	180.45	88.03	64.43
	3	50 (10)	1149.86 ± 8.20	38.5	2.18 ± 0.10	345.98 ± 37.59	28.49 ± 2.20	30.46	240.59	19.39	247.39	193.94	98.59	46.65
		4 (3)	1274.50 ± 94.25	21	2.21 ± 0.11	350.75 ± 30.97	29.02 ± 1.61	13.17	304.56	26.52	248.98	223.79	101.77	80.77
<b>Male</b>	1	38 (9)	432.32 ± 33.25	25.4	1.71 ± 0.08	169.95 ± 19.73	26.94 ± 3.39	24.92	127.60	16.01	124.17	107.17	45.78	20.43
		49 (31)	551.71 ± 51.63	23.5	1.85 ± 0.13	222.14 ± 34.00	29.95 ± 2.69	19.57	178.67	22.82	155.62	137.90	66.52	40.77
	2	46 (15)	778.65 ± 14.11	33.33	1.95 ± 0.12	246.98 ± 36.78	26.65 ± 1.50	28.52	176.54	16.30	181.16	147.76	65.81	28.78
		33 (25)	928.00 ± 39.68	26.27	2.09 ± 0.14	316.88 ± 53.31	29.11 ± 2.04	18.13	259.43	21.94	224.63	202.51	92.25	56.92
	3	54 (18)	1144.46 ± 12.83	37.25	2.22 ± 0.12	343.06 ± 45.41	26.15 ± 2.08	26.78	251.19	15.56	253.34	212.10	89.71	39.08
		25 (22)	1311.88 ± 38.77	23.43	2.45 ± 0.13	468.40 ± 77.70	27.13 ± 1.51	17.98	384.18	21.14	341.31	302.97	127.09	81.22

males (McLaren 1993), the approximate length at which the second period of accelerated growth occurs. We also incorporated a seasonal component to the growth function using an annual periodicity component in combination with the original vB equation. This seasonal component was added by including a sinusoidal function (Eveson et al. 2004):

$$L = L_{\infty}(1 - e^{-k\{a - a_0 + \sin[2\pi(a/365 - w)]\}}) \quad (2)$$

where  $u$  (the amplitude of the wave) and  $w$  (the period) are constants. For each analysis we calculated the information-theoretic evidence ratio (ER, an index of the likelihood of one model over another, calculated as the sample-size corrected Akaike's Information Criteria [ $AIC_c$ ] weight [ $AIC_c w$ ] of the best model divided by  $AIC_c w$  of the next-highest model; Burnham & Anderson 2002) as the basis for examining the relative statistical support for which model fitted the data best for each of the sexes.

To account for any potential bias in the cross-sectional data, we also present longitudinal data for changes in rates of STL gain for seals that were recaptured during consecutive haul-outs ( $n = 104$ ). STL was measured at the start of each haul-out and calculated as a daily rate for the period between the captures. No statistical analyses were possible given the lack of consistent temporal windows among individuals over which growth rates could be calculated.

**Body mass and composition changes.** We compared the body mass ( $n = 470$ ) and composition ( $n = 211$ ) between sexes of 1-, 2- and 3-yr-old seals and between the 2 haul-out periods using generalized linear model (GLM) functions in the R software package (Ver. 2.2.1, R Development Core Team 2004). The models tested for significant effects of main factors (i.e. age, sex and haul-out) and all 2- and 3-way interactions, with body mass or composition as the response variable. Mass data were log-normally distributed, so we log-transformed these for model presentation. Examination of the residual plots suggested that a Gaussian error distribution with an identity link function was the most appropriate for the data.

There was no *a priori* reason to assume that a single model would describe the contribution of terms and their interactions to the response variables, so we used a robust multi-model-inference technique with  $AIC_c$  to select the model(s) that were the best representation of our data (Burnham & Anderson 2002). The selected models are shown with their  $AIC_c w$  to indicate the importance of each model, and the percentage of deviance explained (%DE) as a measure of a model's goodness-of-fit. To determine the effect of any term deemed important in the explained variation in the response variable, we used information-theoretic evidence ratios derived from comparing models differing by only one term (Burnham & Anderson 2002).

## RESULTS

The 2-yr-old seals were the first age group to return for the annual moult (mean arrival date = 28 November  $\pm$  12 d), followed by the 3-yr-olds (5 December  $\pm$  11 d), and finally, the 1-yr-olds (10 December  $\pm$  15 d). Later in the year, the 1-yr-olds returned first for their mid-year haul-out (mean = 22 April  $\pm$  53 d), followed by the 2-yr-olds (4 May  $\pm$  36 d) and the 3-yr-olds (26 May  $\pm$  50 d). The mean body mass and STL of male and female seals ranged from  $167 \pm 22$  kg for 1-yr-olds ( $1.68 \pm 0.09$  m in length) at the start of their annual moult to  $452 \pm 84$  kg ( $2.41 \pm 0.15$  m in length) for 3-yr-olds at the start of their mid-year haul-out. Body size (STL) and mass increased with age (between 1 and 4 yr) and there were some important differences between seasons, and a growth divergence between sexes (Table 1).

### Somatic growth

Male and female seals had similar STLs at 1 yr of age (males =  $1.71 \pm 0.08$  m, females =  $1.69 \pm 0.09$  m), but diverged in length with age. The sinusoidal vB curve (seasonal vB) allowing for seasonal differences fitted the data better than a general vB curve (Fig. 1). Using the  $AIC_c w$  evidence ratio, the seasonal vB growth model improved the fit for males and females ( $ER_{\text{male}} = 198$  and  $ER_{\text{female}} = 1.92$ ), and reduced the residual standard errors (Table 2). This seasonally adjusted vB growth curve shows that males grew rapidly after their annual moult (austral summer), but had reduced

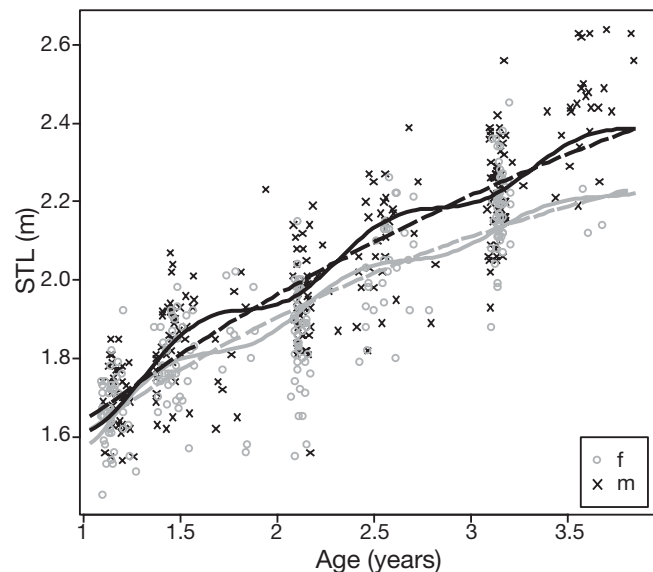


Fig. 1. *Mirounga leonina*. von Bertalanffy (vB) (dashed lines) and seasonal vB (solid lines) growth curves for 1-, 2- and 3-yr-old southern elephant seals (m = males; f = females)

Table 2. *Mirounga leonina*. General and seasonal von Bertalanffy (vB) growth model parameters for juvenile female (n = 225) and male (n = 245) southern elephant seals from Macquarie Island, Southern Ocean.  $k$  and  $a_0$  (theoretical age at which length is 0) are constants;  $u$ : amplitude of the wave;  $w$ : period; na: not applicable

Growth function	$k$	$a_0$	$u$	$w$	Residual SE	df
<b>Females</b>						
vB	0.00079	-758.8	na	na	0.1149	223
Seasonal vB	0.00079	-741.8	46.28	0.18	0.1139	221
<b>Males</b>						
vB	0.00068	-728.8	na	na	0.1256	243
Seasonal vB	0.00068	-752.5	-49.92	0.17	0.1225	241

growth after their mid-year haul-out through the winter. Although females had a seasonal component to growth, this was less pronounced than for males. Furthermore, this seasonal influence appears to have reduced with age. These trends were also reflected in the daily STL growth rate (Fig. 2) based on longitudinal data (n = 104).

**Age and sex differences in size**

As for STL, there were important age, sex and seasonal differences in body mass (Table 1, Fig. 3). The top candidate models showed strong support for age, sex and haul-out effects, with the suggestion of some inter-

actions (Table 3). All main terms had important contributions ( $ER_{age} = 3.0 \times 10^{159}$ ;  $ER_{sex} = 1.3 \times 10^3$ ;  $ER_{haul-out} = 3.2 \times 10^7$ ), but only the sex $\times$ haul-out interaction had some support ( $ER = 256$ ); however, adding this interaction to the single-term model only improved the %DE by approximately 0.5%. All other 2- and 3-way interactions had  $ER < 0.8$ ). Therefore, there were overall increases in mass with age; males were larger than females and seals were larger in the mid-year than in the previous moult (Fig. 3a). The sex $\times$ haul-out interaction was due to male and female masses being more closely aligned during the mid-year haul-out for 1- and 3-yr-olds than during the moult. Similar to somatic growth, males increased in mass more rapidly than

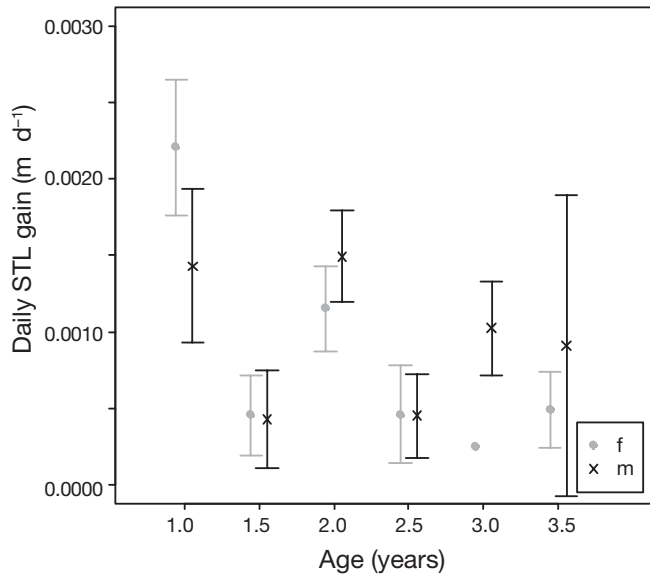


Fig. 2. *Mirounga leonina*. Daily snout-tail length (STL) growth rate during the summer and winter periods for 1-, 2- and 3-year-old southern elephant seals (m = males; f = females) ( $\bar{x} \pm 2 \times SE$ ) from longitudinal data

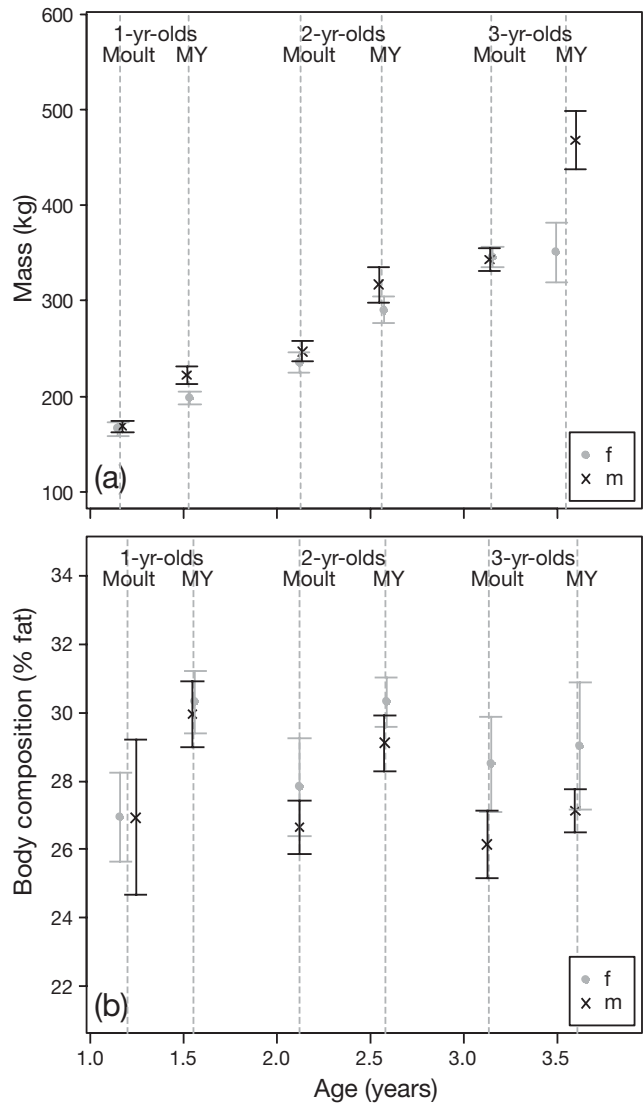


Fig. 3. *Mirounga leonina*. (a) Body mass and (b) body composition (% fat) at the start of the moult and mid-year (MY) haul-outs for 1-, 2- and 3-year-old southern elephant seals (m = males; f = females) ( $\bar{x} \pm 2 \times SE$ ) from longitudinal data



Table 3. *Mirounga leonina*. Top candidate generalized linear models (GLM) describing the contributions of age (a), sex (s) and haul-out (h) and their interactions with body mass and composition of juvenile southern elephant seals. Also shown are the sample-size-adjusted Akaike Information Criterion weights ( $AIC_cw$ ) and the percentage of deviance explained (%DE) for each model

Response	Model	$AIC_cw$	%DE
Mass	a + s + h + s × h	0.4322	80.496
	a + s + h + s × h + a × h	0.2480	80.535
	a + s + h + a × s + s × h	0.1557	80.497
	a + s + h + a × s + a × h + s × h	0.0892	80.536
	a + s + h + a × s + a × h + s × h + a × s × h	0.0702	80.602
	a + s + h	0.0025	79.976
Body composition	a + s + h + a × h + a × s	0.5182	33.903
	a + s + h + a × s + a × h + s × h	0.2030	34.986
	a + s + h + a × h	0.1189	32.297
	a + s + h + a × s + a × h + s × h + a × s × h	0.0726	34.019
	a + s + h + a × h + s × h	0.0484	32.401
	a + s + h + a × s	0.0260	31.317
	a + s + h	0.0015	28.729

females in the summer, but then did not increase in mass at a similar rate during the winter.

There were also age, sex and haul-out differences in body composition (BC; Fig. 3b). The top candidate models showed strong age, sex and haul-out effects (Table 3;  $ER_{age} = 62$ ;  $ER_{sex} = 73$ ;  $ER_{haul-out} = 2.1 \times 10^{11}$ ), and support for age × sex ( $ER = 4.2$ ) and age × haul-out ( $ER = 22.4$ ) interactions. There was no evidence for sex × haul-out or 3-way interactions (all  $ER < 0.4$ ) The 1-yr-old seals returned for their moult and mid-year haul-outs, and their BCs differed between these seasons ( $26.9 \pm 2.7\%$  and  $30.1 \pm 2.6\%$  respectively), although male and female BCs were similar at these times. However, as individuals aged, male and female BCs diverged more noticeably, with females having a greater proportion of fat than males.

### Modelled rates of mass gain

To describe rates of body mass, lean mass and fat mass gain (Table 4, Fig. 4) for an average seal during the winter and summer, we used the overall mean body masses and BCs of the different-aged seals at the start of the moult and mid-year haul-outs, and mean haul-out durations, proportion of mass loss and BCs at the end of the respective haul-outs (Table 1). These modelled data clearly show that during summer the rates of body, lean and fat mass gain are almost double those observed during winter. Overall mass gain shows a similar pattern, with somatic growth increasing in summer and diverging between males and females. However, changes in mass gain for lean and fat

tissue may be more important ecologically. For lean mass, males had increased gain in summer, but lower gain in winter than females. For fat mass there was again a similar pattern: males gained more fat mass in summer, although in winter their fat mass gain was similar to that of females.

### DISCUSSION

To maximize their long-term fitness, animals need to find an optimal strategy for partitioning energy between daily maintenance, somatic growth, and storage. This optimal strategy is unlikely to remain constant throughout an individual's development; instead, it will need continuous adjustment as these conflicting

Table 4. *Mirounga leonina*. Overall mass, lean mass and fat mass gains over their summer and winter trips to sea for 1-, 2- and 3-yr-old southern elephant seals

Age	Season	Time at sea (d)	Overall mass gain (kg)	Lean mass gain (kg)	Fat mass gain (kg)	Mass gain ( $kg d^{-1}$ )	Lean mass gain ( $kg d^{-1}$ )	Fat mass gain ( $kg d^{-1}$ )
<b>Female</b>								
1	Summer	108.97	85.25	44.24	41.00	0.78	0.41	0.38
	Winter	190.43	73.57	46.87	26.70	0.39	0.25	0.14
2	Summer	133.45	135.77	75.12	60.64	1.02	0.56	0.45
	Winter	189.29	101.10	66.94	34.16	0.53	0.35	0.18
3	Summer	86.14	110.16	55.03	55.12	1.28	0.64	0.64
<b>Male</b>								
1	Summer	94.00	94.55	48.45	46.10	1.01	0.52	0.49
	Winter	203.44	68.31	43.27	25.04	0.34	0.21	0.12
2	Summer	116.02	140.34	76.87	63.47	1.21	0.66	0.55
	Winter	190.19	83.63	50.83	32.80	0.44	0.27	0.17
3	Summer	130.17	217.21	129.21	88.00	1.67	0.99	0.68

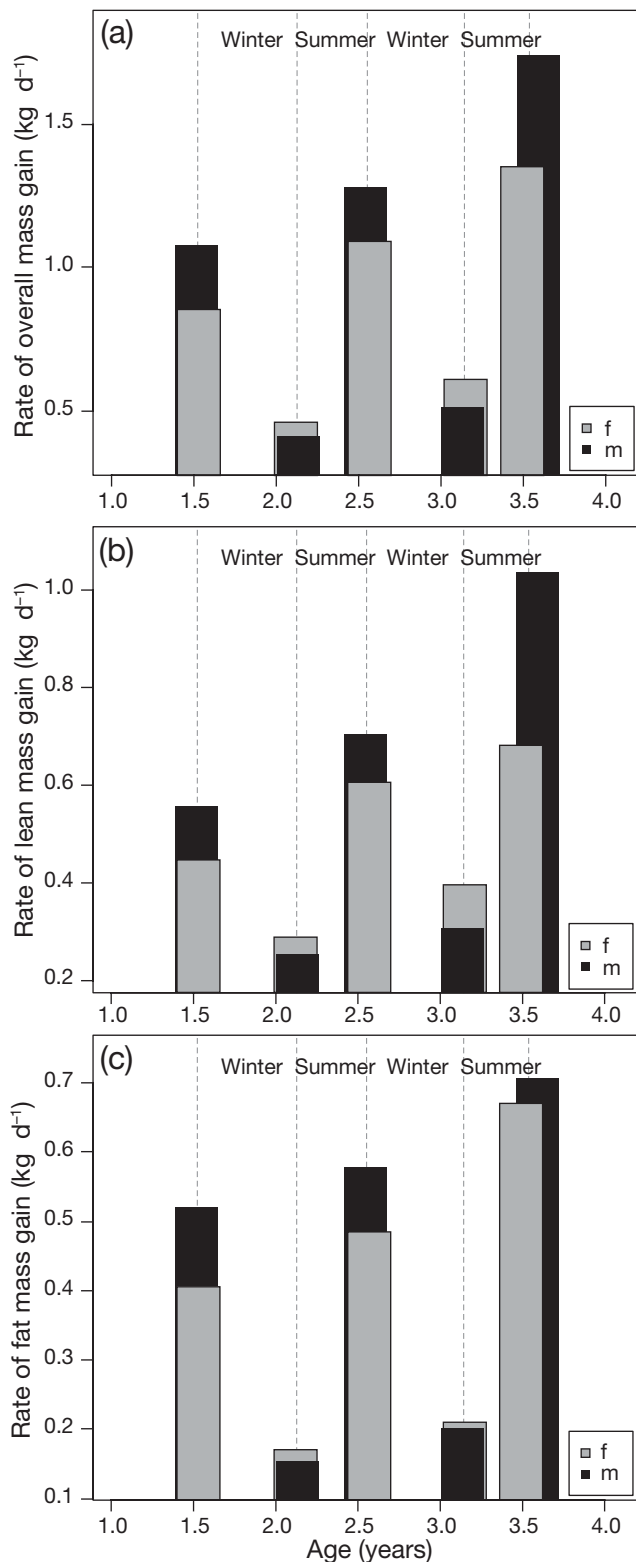


Fig. 4. *Mirounga leonina*. Rates of (a) overall mass, (b) lean mass and (c) fat mass gain during summer and winter trips to sea for 1-, 2- and 3-yr-old southern elephant seals. Grey dashed lines delineate the different seasons. (m = males; f = females)

demands change. Ultimately, the amount of energy allocated towards growth can influence both the probability of survival and, in the long term, reproductive success. Furthermore, whatever the overall strategy, animals must be able to adjust their energy budgets to seasonal variation in food availability and quality. Although seasonal differences in growth have been found for many species (Stearns 1992), these are often related either to reproductive or physiological state (intrinsic factors) or to environmental influences (extrinsic factors). There have been few studies examining the factors that influence growth simultaneously (once energy stores provided by maternal investment have been depleted) which would have large effects on an individual's survival and on population demography (Lindström 1999, Crocker et al. 2006). Southern elephant seals are long-lived predators that are active throughout the year during which time the long winter foraging migration (and moult haul-out) is followed by a shorter summer foraging migration (and mid-year haul-out). Foraging in an extremely seasonal near-polar environment during these 2 phases therefore leads to the prediction that both seasonal and intrinsic factors play a complex and integrated role in dictating observed growth patterns.

Seasonality in environmental conditions is a major influence on growth for many species (Stearns 1992, Lindström 1999) through climatic changes that influence the energetic cost of thermoregulation (Sand 1996) and alter the availability or quality of food (Collins & Rodhouse 2006). Primary productivity in the Southern Ocean is highly seasonal due to strong fluctuations in light intensity and ice cover (Arrigo et al. 1998) and influences the body condition and reproductive state of grazers such as Antarctic krill *Euphausia superba* (Kawaguchi et al. 2006). Juvenile southern elephant seals from Macquarie Island spend around 90% of their time south of the Polar Front in summer and the majority (around 75%) of their time in winter between the Polar Front and the southern boundary of the Antarctic Circumpolar Current (Field et al. 2004). Although little is known about the distribution of elephant seal prey in the Southern Ocean (Rodhouse & White 1995), especially during winter, we have shown that juvenile seals grow faster in summer than in winter. Furthermore, our modelled data suggest that although the average time an individual spends at sea during winter is longer than during the summer trip (Field et al. 2005a), summer mass gain is almost double winter mass gain. Although there is likely to be an intrinsic seasonal influence on mass gain, due to differences in energy use and storage resulting from different physiological processes operating during the moult and mid-year haul-outs (Field et al. 2005b), we suggest that the greatest difference between summer and win-

ter mass gains is due to reduced prey quality or availability in winter (Collins & Rodhouse 2006). This may be especially true for younger seals that may be unable to penetrate the denser pack ice in more southerly waters, due to physiological or thermoregulatory constraints this environment poses. Indeed, inter-annual variability in southern elephant seal weaning mass can be explained, in part, by variation in sea ice extent south of Macquarie Island (McMahon & Burton 2005) that influences the region's productivity (Arrigo et al. 1998) during the key foraging period of pregnant females. We suggest further that this over-winter foraging period represents an energy-limiting time for juvenile seals beyond their first year of life.

For many species, seasonal variation in growth patterns has been attributed to differences due to sex, age and physiological or reproductive state (Warrick & Cypher 1999, Beck et al. 2003, Peltier & Barboza 2003, Veiberg et al. 2004). All juvenile mammals need to reach a certain anatomical size and body condition to reproduce successfully, but the rate at which they do so may influence their age at primiparity, lifetime fecundity or the probability of survival (Post & Parkinson 2001, McMahon et al. 2003). For juvenile southern elephant seals there are 2 main intrinsic influences on growth: (1) the allocation of energy for maintenance, thermoregulation, diving and moulting and, (2) although not directly related to breeding, the differential energy allocation for reproductive size and condition associated with this species' sexual dimorphism. In other words, juveniles are forced to balance the energy allocated to growth against storage during periods of resource scarcity (while ashore or at sea) or additional metabolic costs (e.g. moulting or foraging). Juvenile southern elephant seals fare relatively well in summer when they experience increased growth rates and accumulate more energy reserves. However, after their winter foraging trip they return with a greater proportion of lean tissue to blubber and a reduced overall mass gain. Although this may be due in part to reduced availability or quality of food, it may also be influenced by the extra energy required for moulting. This process requires more protein for the production of new epidermis and higher metabolic costs and heat loss associated with increased blood perfusion to the skin (Ling 1974). As such, the resultant increasing energy loss may leave juveniles incapable of maintaining high rates of somatic growth preceding and during this time.

Body size increases reproductive success in highly dimorphic species (Stearns 1992), where larger males have higher reproductive success (Clinton & Le Boeuf 1993). For most pinnipeds, early growth and survival is influenced by maternal energy expenditure (McMahon et al. 2003). After accounting for variation in parental expenditure, the time taken for a juvenile to reach reproductive size and condition may be the most important

determinant of lifetime breeding success and survival (Lindström 1999). A recent review of sexual segregation (Ruckstuhl & Neuhaus 2000) highlighted the potential of differential activity budgets (e.g. in foraging) to influence the allocation of resources for maintenance, offspring provisioning or growth. Similar segregation has been shown for juvenile southern elephant seals in terms of habitat use (Field et al. 2005a) and metabolic differences (Field et al. 2005b), which may thus influence growth. We propose then that selection has favoured sex-specific growth strategies whereby males take more risks when foraging to increase early growth, whereas females select less risky foraging strategies to minimize potential variation in diet that will have negative consequences for the survival of their future offspring.

We suggest that these different growth strategies are in response to differences in energy use (Field et al. 2005b). Initially, 1-yr-old male and female body masses and energy reserves are similar. During the austral summer, all juveniles increase in length and body mass, but they also increase their blubber stores. During winter, however, 2 different growth strategies related to energy allocation emerge. Juvenile females continue to grow in length and mass while storing energy mostly as blubber. Males grow more slowly, but they become longer and leaner by allocating relatively more energy to lean tissue growth. Overall, these physiological strategies enable males to increase body size more quickly than females, while females use less and store greater proportions as fat (Field et al. 2005b) in preparation for earlier maturity and the onset of breeding. Furthermore, an increase in body size has been shown to increase dive duration (Hindell et al. 1999) and depth capacity, and alter diet composition (Field et al. 2006); these trends, when combined with ontogenetic spatial segregation at sea, reduce the potential for intra-specific competition (Field et al. 2005a).

The evolution of different growth strategies appears to provide the sexes with the means to maximise their long-term reproductive success when exploiting food resources in an extremely variable and seasonal environment. The female strategy of moderate growth to reproductive size and condition maximizes the probability of reaching breeding age (Festa-Bianchet et al. 2000 and references therein) where greater energy stores may be required to buffer females from periods of low availability or poorer quality of food. Alternatively, males increase the relative allocation of energy to somatic growth to attain a mating advantage, despite having a decreased probability of survival during times of reduced resource availability. Indeed, lower male survival (McMahon et al. 2003) during periodic poor-resource years may result from their need for greater blubber reserves to survive during periods of



fasting on land or at sea (McConnell et al. 2002) when the smaller, fatter females are prone to do better.

Juveniles are potentially the component of the population most sensitive to variation in environmental factors affecting resource availability (Lindström 1999). Evidence from this study, combined with at-sea spatial use (Field et al. 2005a), suggests that juveniles possess differential growth and habitat-use strategies that assist in reducing intra-specific competition for resources and promote optimal resource allocation for growth and maintenance, thereby increasing an individual's probability of survival and future breeding success. We suggest that a decrease in food availability and an increased requirement for protein use and storage in winter results in a reduction in the energy available for growth. This is likely to contribute to (1) a reduction in winter survival for males and (2) a delay in the age at primiparity for females. These results provide strong evidence for the proximate physiological mechanisms responsible for driving demographic patterns in long-lived, sexually dimorphic species living in challenging environments.

**Acknowledgements.** We thank M. Biuw, J. Harrington, C. McKinley, N. Milius, R. Munro, M. Pauza, and K. Wheatley and members of the 51st to 53rd ANARE to Macquarie Island for their assistance during fieldwork. We thank the Australian Antarctic Division and J. van den Hoff for logistic support. We also thank P. Eveson (CSIRO Marine Laboratory, Hobart) for guidance in fitting seasonal growth curves to our data. M. Biuw and 2 anonymous reviewers provided helpful comments to improve the manuscript. Funding was provided by the Antarctic Science Advisory Committee (ASAC) and Sea World Research and Rescue Foundation Inc. (SWRRFI). Data were collected with Australian Antarctic Animal Ethics Committee approval (ASAC 2265 and 1171) and with Tasmanian Parks and Wildlife Service permits.

#### LITERATURE CITED

- Arrigo KR, Worthen D, Schnell A, Lizotte MP (1998) Primary production in Southern Ocean waters. *J Geophys Res* 103 (C8):15587–15600
- Beck CA, Bowen WD, Iverson SJ (2003) Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. *J Anim Ecol* 72:280–291
- Bell CM, Burton HR, Lea MA, Hindell MA (2005) Growth of female southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Polar Biol* 28:395–402
- Boyce MS (1985) Evolution of life histories: theory and patterns from mammals. In: Boyce MS (ed) *Evolution of life histories: theory and patterns from mammals*. Yale University Press, New Haven, CT, p 3–32
- Boyd IL (2000) State-dependent fertility in pinnipeds: contrasting capital and income breeders. *Funct Ecol* 14: 623–630
- Bradshaw CJA, Hindell MA, Best NJ, Phillips KL, Wilson G, Nichols PD (2003) You are what you eat: describing the foraging ecology of southern elephant seals (*Mirounga leonina*) using blubber fatty acids. *Proc R Soc Lond B* 270: 1283–1292
- Brafield AE, Llewellyn MJ (1982) *Animal energetics*. Blakie, Glasgow
- Burnham KP, Anderson DR (2002) *Model selection and multimodal inference: a practical information-theoretic approach*, 2nd edn. Springer-Verlag, New York
- Caughley G, Sinclair ARE (1994) *Wildlife ecology and management*. Blackwell Scientific, Boston, MA
- Clinton WL, Le Boeuf BJ (1993) Sexual selection's effects on male life history and the pattern of male mortality. *Ecology* 74:1884–1892
- Collins MA, Rodhouse PGK (2006) Southern Ocean cephalopods. *Adv Mar Biol* 50:192–263
- Crocker DE, Costa DP, Le Boeuf BJ, Webb PM, Houser DS (2006) Impact of El Niño on the foraging behavior of female northern elephant seals. *Mar Ecol Prog Ser* 309: 1–10
- Eveson JP, Laslett GM, Polacheck T (2004) An integrated model for growth incorporating tag-recapture, length-frequency, and direct aging data. *Can J Fish Aquat Sci* 61: 292–306
- Festa-Bianchet M, Jorgenson JT, Réale D (2000) Early development, adult mass and reproductive success in bighorn sheep. *Behav Ecol* 11:633–639
- Field IC, Bradshaw CJA, McMahon CR, Harrington J, Burton HR (2002) Effects of age, size and condition of elephant seals (*Mirounga leonina*) on their intravenous anaesthesia with tiletamine and zolazepam. *Vet Rec* 151:235–240
- Field IC, Bradshaw CJA, Burton HR, Hindell MA (2004) Seasonal use of oceanographic and fisheries management zones by juvenile southern elephant seals (*Mirounga leonina*) from Macquarie Island. *Polar Biol* 27:432–440
- Field IC, Bradshaw CJA, Burton HR, Sumner MD, Hindell MA (2005a) Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals. *Oecologia* 142:127–135
- Field IC, Bradshaw CJA, Burton HR, Hindell MA (2005b) Juvenile southern elephant seals exhibit seasonal differences in energetic requirements and use of lipids and protein stores. *Physiol Biochem Zool* 78:491–504
- Field IC, Bradshaw CJA, van den Hoff J, Burton HR, Hindell MA (2006) Age related shifts in the diet composition of southern elephant seals expand overall foraging niche. *Mar Biol* doi:10.1007/s00227-006-0417-y
- Gales NJ, Burton HR (1987) Ultrasonic measurement of blubber thickness of the southern elephant seal *Mirounga leonina* (Linn.). *Aust J Zool* 35:207–217
- Hall AJ, McConnell BJ, Barker RJ (2001) Factors affecting first-year survival in grey seals and their implications for life history strategy. *J Anim Ecol* 70:138–149
- Hindell MA, Slip DJ, Burton HR (1994) Possible causes of the decline of southern elephant seal populations in the Southern Pacific and Southern Indian Oceans. In: Le Boeuf BJ, Laws RM (eds) *Elephant seals: population ecology, behavior, and physiology*. University of California Press, Berkeley, CA, p 66–84
- Hindell MA, McConnell BJ, Fedak MA, Slip DJ, Burton HR, Reijnders PJH, McMahon CR (1999) Environmental and physiological determinants of successful foraging by naive southern elephant seal pups during their first trip to sea. *Can J Zool* 77:1807–1821
- Kawaguchi S, Candy SG, King R, Naganobu M, Nicol S (2006) Modelling growth of Antarctic krill. I. Growth trends with sex, length, season and region. *Mar Ecol Prog Ser* 306:1–15
- Lindström J (1999) Early development and fitness in birds and mammals. *Trends Ecol Evol* 14:343–348

- Ling JK (1974) The integument of marine mammals. In: Harrison RJ (ed) Functional anatomy of marine mammals, Vol 2. Academic Press, London, p 1–44
- McConnell B, Fedak M, Burton HR, Engelhard GH, Reijnders PJH (2002) Movements and foraging areas of naïve, recently weaned southern elephant seal pups. *J Anim Ecol* 71:65–78
- McLaren IA (1993) Growth in pinnipeds. *Biol Rev* 68:1–79
- McMahon CR, Burton HR (2005) Climate change and seal survival: evidence for environmentally mediated changes in elephant seal, *Mirounga leonina*, pup survival. *Proc R Soc Lond B* 272:1471–2954
- McMahon CR, Burton H, McLean S, Slip D, Bester M (2000) Field immobilisation of southern elephant seals with intravenous tiletamine and zolazepam. *Vet Rec* 146:251–254
- McMahon CR, Burton HR, Bester MN (2003) A demographic comparison of two southern elephant seal populations. *J Anim Ecol* 72:61–74
- McMahon CR, Bester MN, Burton HR, Hindell MA, Bradshaw CJA (2005) Population status, trends and a re-examination of the hypotheses explaining the recent decreases of the southern elephant seal, *Mirounga leonina*. *Mamm Rev* 35: 82–100
- Mellish JE, Tuomi PA, Horning M (2004) Assessment of ultrasound imaging as a noninvasive measure of blubber thickness in pinnipeds. *J Zoo Wildl Med* 35:116–118
- Peltier TC, Barboza PS (2003) Growth in an Arctic grazer: effects of sex and dietary nitrogen on yearling muskoxen. *J Mammal* 84:915–925
- Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge
- Post JR, Parkinson EA (2001) Energy allocation strategy in young fish: allometry and survival. *Ecology* 82:1040–1051
- R Development Core Team (2004) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rintoul SR, Donguy JR, Roemmich DH (1997) Seasonal evolution of upper ocean thermal structure between Tasmania and Antarctica. *Deep-Sea Res I* 44:1185–1202
- Rodhouse PG, White MG (1995) Cephalopods occupy the ecological niche of epipelagic fish in the Antarctic polar frontal zone. *Biol Bull* 189:77–80
- Ruckstuhl KE, Neuhaus P (2000) Sexual segregation in ungulates: a new approach. *Behaviour* 137:361–377
- Sand H (1996) Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity and environmental conditions. *Oecologia* 106:212–220
- Slip DJ, Gales NJ, Burton HR (1992) Body mass loss, utilisation of blubber and fat, and energetic requirements of male southern elephant seals, *Mirounga leonina*, during the moulting fast. *Aust J Zool* 40:235–243
- Stearns SC (1992) The evolution of life histories. Oxford University Press, Oxford
- Veiberg V, Egil Loe L, Myrsterud A, Langvatn R, Stenseth N (2004) Social rank, feeding and winter weight loss in red deer: any evidence of interference competition? *Oecologia* 138:135–142
- Warrick GD, Cypher BL (1999) Variation in body mass of San Joaquin kit foxes. *J Mammal* 80:972–979
- Webb PM, Crocker DE, Blackwell SB, Costa DP, Le Boeuf BJ (1998) Effects of buoyancy on the diving behavior of northern elephant seals. *J Exp Biol* 201:2349–2358

*Editorial responsibility: Rory Wilson (Contributing Editor), Swansea, UK*

*Submitted: February 28, 2006; Accepted: July 12, 2006  
Proofs received from author(s): January 25, 2007*