

Influence of maternal mass and condition on energy transfer in Weddell seals

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Summary

1. Environmental variation influences food abundance and availability, which is reflected in the reproductive success of top predators. We examined maternal expenditure, offspring mass and condition for Weddell seals in 2 years when individuals exhibited marked differences in these traits.
2. For females weighing ≥ 355 kg there was a positive relationship between maternal post-partum mass (MPPM) and lactation length, but below this there was no relationship, suggesting that heavier females were able to increase lactation length but lighter females were restricted to a minimum lactation period of 33 days.
3. Overall, females were heavier in 2002, but in 2003 shorter females were lighter than similar-sized females in 2002 suggesting that the effects of environmental variability on foraging success and condition are more pronounced in smaller individuals.
4. There was no relationship between MPPM and pup birth mass, indicating pre-partum investment did not differ between years. However, there was a positive relationship between MPPM and pup mass gain. Mass and energy transfer efficiency were 10.2 and 5.4% higher in 2002 than 2003, which suggests costs associated with a putatively poor-resource year were delayed until lactation.
5. Heavier females lost a higher proportion of mass during lactation in both years, so smaller females may not have been able to provide more to their offspring to wean a pup of similar size to larger females.
6. MPPM had only a small influence on total body lipid; therefore, regardless of mass, females had the same relative body composition. Females with male pups lost a higher percentage of lipid than those with female pups, but by the end of lactation female pups had 4.5% higher lipid content than males.
7. It appears that for Weddell seals the consequences of environmentally induced variation in food availability are manifested in differences in maternal mass and expenditure during lactation. These differences translate to changes in pup mass and condition at weaning with potential consequences for future survival and recruitment.

Key-words: body composition, lactation, *Leptonychotes weddellii*, maternal expenditure, phocids

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Introduction

In many mammals lactation represents a period of extreme demand on energy reserves (Gittleman & Thompson 1988; Rogowitz 1996). Young mammals are born nutritionally dependent and therefore exert high

energetic demands on mothers during lactation. Mammals have developed two main strategies to support the energetic costs of lactation: 'capital breeding' relies largely on stored body reserves, while 'income breeding' relies on more-recently acquired energy. The costs and benefits of these alternative resource-use strategies differ depending on the timing and variability of resource availability (Boyd 2000). Long-lived mammals must therefore have the ability to locate food in successive years and in environments where the temporal predictability of food patches can be low (McCafferty *et al.* 1998; Planque & Taylor 1998; Constable *et al.* 2000).

Annual variation in foraging success influences body reserves, which in turn influences current and future reproduction (Croxall, Reid & Prince 1999; Beauplet *et al.* 2004; Lynnes, Reid & Croxall 2004). The evolution of reproductive strategies is driven by a balance between the costs incurred by the parents through investment in offspring, and the value they obtain from this investment in terms of their offspring's subsequent reproductive output (Shuster & Wade 2003). To understand fully how mammals translate variability in resources to reproductive output, data on key demographic and physiological parameters such as the quantification of energy transfer, assimilation efficiency, resource allocation and survival are needed.

In marine ecosystems, high interannual variability in resource abundance is the norm resulting from cyclic environmental patterns (e.g. El-Niño-Southern Oscillation) and unpredictable fluctuations in oceanographic conditions (Pinaud & Weimerskirch 2002). This variability can affect all trophic levels, but upper trophic level species are sometimes regarded as 'ecosystem indicators' on the notion that such proximate (environmental) factors will affect their diet, reproductive performance and population size (Hindell *et al.* 2003; Le Boeuf & Crocker 2005; Reid *et al.* 2005). Examining the biological consequences of environmental change (Bradshaw *et al.* 2000; Barbraud & Weimerskirch 2001; Thompson & Ollason 2001; Beauplet *et al.* 2004) may improve our understanding of how predators respond to changes in the distribution of marine resources as the result of global climate change or commercial exploitation.

Most marine ecosystem studies have focused on environmental change and population dynamics of seabirds (e.g. Croxall, Trathan & Murray 2002; Pinaud, Chérel & Weimerskirch 2005). However, demographic variation between species suggests that we should not expect all marine predators to respond to environmental change in the same way (Croxall 1992). Phocid seals are one of the few groups of mammals within which some species exhibit extreme capital breeding where females meet the energy requirements of lactation solely through stored body reserves. Although a temporal separation exists between energy acquisition and maternal expenditure, there is often a spatial separation as well, with females remaining on land or ice. The physiology of lactation is influenced strongly by the constraints

resulting from this division between foraging and reproduction (Crocker & Costa 2001a). Fluctuations in energy acquisition prior to the breeding season are expressed as variation in maternal mass and condition. These may impose energetic constraints that influence both the duration and magnitude of maternal expenditure measured in terms of pup birth mass and growth (Pomeroy *et al.* 1999; Crocker *et al.* 2001b; McMahon & Burton 2005). In turn, pup growth will have consequences for survival (McMahon, Burton & Bester 2000; Hall, McConnell & Barker 2001) and ultimately, the lifetime reproductive success of mothers (Trillmich 1996). Therefore, the amount of resources available and possibly some expectation of future resource availability may influence maternal expenditure. As a result, quantifying the ecological and physiological aspects of lactation offers an opportunity to measure immediate (short time lag) responses to environmental change.

Weddell seals *Leptonychotes weddellii* (Lesson) are long-lived, upper trophic level predators in the Southern Ocean. They are the only phocid to inhabit these high latitudes year-round and are easily accessible during the breeding and moulting periods when they haul out at predictable cracks in the fast-ice (Kooyman 1981). Their ability to cope with polar conditions and their accessibility makes them excellent candidates to study constraints on lactation. Like all large phocids, Weddell seals deposit subcutaneous fat during the nonbreeding season and then use this stored energy for milk production and maintenance during the lactation period. However, the 6–7-week lactation period of Weddell seals (Tedman & Bryden 1979) is different from other phocids (see Trillmich 1996 for a review) given that it is one of the longest recorded, especially compared with that of similar-sized species (elephant seals *Mirounga* spp., 22–28 days).

For most phocid species, pups are weaned abruptly and must learn to swim and dive on their own. However, Weddell seal pups are introduced to the water during lactation (starting at 10–12 days) when they accompany mothers during short bouts of diving (Stirling 1969). Some females also forage during lactation (Hindell *et al.* 2002; Sato *et al.* 2002; Eisert *et al.* 2005), but the reasons for this are still unclear. This behaviour is unique in that most other phocids fast for the entire duration of lactation, and those that do forage are considerably smaller (harbour seal *Phoca vitulina* – Bowen *et al.* 2001) with relatively limited body stores and higher relative energy expenditure (Bowen *et al.* 2001). So the question remains as to why a larger phocid should need to forage during lactation.

In this study, we measured maternal post-partum mass (MPPM) and body composition of Weddell seals at the beginning of the breeding season as an indicator of overwinter foraging success for two consecutive years. We examined how MPPM and body condition related to a mother's energy allocation and the growth of her pup, and whether this relationship differed between years. We hypothesized that when maternal

mass is relatively low these individuals should transfer less mass and energy to the pup during lactation. In turn, we expected that these differences in provisioning would have detectable consequences on pup growth rate, condition and survival.

Methods

This study was done at Hutton Cliffs, Antarctica (77°51'S, 166°45'E) during the 2002 and 2003 breeding seasons (October to December). Thirty mother–pup pairs in 2002 and 25 pairs in 2003 were captured 1–6 (mean 3.8 ± 0.22) days post-partum. Females were chosen randomly from the 60–100 females usually present at this site. Individual females were identified by flipper tags attached in previous years and pups born to study females were marked with hind flipper tags soon after birth as part of a long-term tagging study (Cameron & Siniff 2004). Age was known for 19 females in 2002 and 21 females in 2003.

Weaning was defined as when the pup was seen alone for ≥ 4 days, with multiple surveys throughout the day. Owing to restrictions of working on fast-ice, not all weaning dates could be determined accurately, and mother–pup pairs were captured 34–43 (37.4 ± 0.40) days post-partum. However, some females remained up to 6 days after capture. For statistical comparisons requiring absolute measurements (as opposed to rates), parameters of both females and pups were extrapolated to weaning based on a linear relationship between MPPM and lactation length for the females with known weaning dates ($n = 32$; $y = 0.07x + 6.98$; see Results).

MATERNAL BODY MASS AND COMPOSITION

We used isotopically labelled water to measure body composition of females and their pups at the post-parturition (PP) and end-lactation (EL) periods. Once captured, each female was immobilized by an intravenous injection of Telazol® (combination of 1 : 1 tiletamine/zolazepam, Fort Dodge, Castle Hill, NSW, Australia), at an average dose of 0.6 mg kg^{-1} into the extradural vein, or intramuscularly at an average dose of 1.0 mg kg^{-1} in the rear flank. Females were weighed to the nearest 1 kg. Standard body length and six girth measurements (Field *et al.* 2002) were recorded for all females.

After immobilization, a 10-mL blood sample was collected in heparinized vacutainers to measure background isotope levels. Immediately after, a preweighed dose (to the nearest 0.1 mg) of approximately 222 MBq of tritiated water (HTO) was administered to each female. Owing to a shortage of HTO at the beginning of the 2002 field season, 10 females were administered a dose of deuterium oxide (HDO, specific concentration: 99.8%) at the PP capture while HTO was used for all other females and the EL captures. The syringe was flushed with blood twice to ensure complete isotope delivery. During equilibration, mothers were prevented

from entering the water by blocking access to the nearest water holes. A second blood sample (10 mL) was taken 150 min on average after initial injection to determine enrichment level. Equilibration occurs in southern elephant seal *Mirounga leonina* (Linnaeus) females within 90 min of administration (intravenously; M.A. Hindell, unpublished data), so we were confident equilibration was achieved in all cases. All procedures were repeated near the end of lactation.

Body mass and composition measured after the day of birth were interpolated to estimate MPPM and composition using calculated rates of daily loss for each individual. For females that were captured only at PP ($n = 14$), body composition was adjusted to birth values by taking the average change in total body water (TBW $\text{g}^{-1} \text{ day}^{-1}$) of females with multiple captures.

PUP BODY MASS AND COMPOSITION

Each pup was weighed to the nearest 0.5 kg and body length and axial girth were measured. Body composition was measured for all pups ($n = 25$) at PP in 2003 and for 25 and 22 pups at EL in 2002 and 2003, respectively. A 10-mL blood sample was collected to measure background isotope enrichment levels. A preweighed dose of approximately 74 MBq of HTO in 2002, and a 10-mL dose of HDO (specific concentration: 99.8%) in 2003 was administered subsequently to each pup. Pups were prevented from suckling during the equilibration period (average = 150 min), after which a second blood sample was taken.

Plasma was separated and stored at -20°C . Owing to high TBW content (low total body lipid; TBL) and analytical errors, some measurements of body composition at PP were implausibly low (i.e. $\text{TBL} < 3\%$, $n = 6$). Therefore, all values greater than 3% were averaged to give a mean body composition at birth, which was applied to all pups in 2002 and those pups in 2003 with values below 3%. With such low TBL values at birth we believe this averaging would not introduce a large amount of error in further calculations. The TBL values greater than 3% corresponded to a TBW of $< 70\%$ and Tedman & Green (1987) found similar values at birth (mean = 72.5%).

SAMPLE ANALYSIS

Plasma samples were analysed for HTO activity using liquid scintillation spectrometry. Plasma samples (100 μL) were distilled in triplicate using the method of Ortiz, Costa & Le Boeuf (1978). For each vial of water recovered, 4 mL of Eco-lite scintillate was added and HTO activity was counted for 15 min using a Beckman LS6500 scintillation counter. Mass spectrometric analysis of deuterium enrichment was done in triplicate using H_2 gas and a platinum-on-alumina catalyst according to the methodology described in Scrimgeour *et al.* (1993).

DATA ANALYSIS

Measuring TBW by dilution space consistently overestimates water volume (Reilly & Fedak 1990; Lydersen, Hammill & Ryg 1992; Arnould, Boyd & Speakman 1996); therefore, we calculated TBW by multiplying the isotope dilution space by a correction factor (HTO: 4.0%, and HDO: 2.8%) derived for grey seals (*Halichoerus grypus* – Reilly & Fedak 1990).

Per cent total body lipid (%TBL), per cent total body protein (%TBP) and total body gross energy (TBGE) were then estimated from body mass (M_b) and TBW according to equations of Reilly & Fedak (1990):

$$\%TBL = 105.1 - (1.47 \times \%TBW) \quad \text{eqn 1}$$

$$\%TBP = (0.42 \times \%TBW) - 4.75 \quad \text{eqn 2}$$

$$TBGE (MJ) = (40.8 \times M_b) - (48.5 \times TBW) - 0.4 \quad \text{eqn 3}$$

Four females in 2002 and five pups in 2003 were injected with HTO and HDO simultaneously to compare both techniques for measuring TBW. In each case the estimated value of TBW was higher from HDO than from HTO dilution (differences for females: $6.05 \pm 0.02\%$; pups: $5.69 \pm 0.01\%$). For between-year comparisons, all values derived from HDO analyses were corrected for direct comparison with HTO values.

A series of generalized linear models (GLM) were constructed to examine intraspecific and interannual differences of females and pups. Examination of the residuals for all models determined the statistical error distribution and link function most appropriate for each analysis. Model selection was based on Akaike's Information Criteria corrected for small samples (AIC_c , Burnham & Anderson 2002). AIC_c values were ranked, with the most parsimonious model(s) having the lowest AIC_c values and highest model weights. From a set of a priori models we used predictive model-averaging to determine the magnitude of the effect of some terms, keeping all other dependent variables constant (Burnham & Anderson 2002). Percentages were not arcsine transformed prior to analyses because most values fell between 30 and 70%. The information-theoretic weight of evidence (w_{+i}) for each predictor was calculated by summing the model AIC_c weights (w_i) over all models in which each term appeared. However, the w_{+i} values are relative, not absolute because they will be > 0 even if the predictor has no contextual explanatory importance (Burnham & Anderson 2002). To judge which predictors were relevant to the data at hand, a baseline for comparing relative w_{+i} across predictors was required, so we randomized the data for each predictor separately, recalculated w_{+i} , and repeated this procedure 100 times for each predictor. The median of this new randomized w_{+i} distribution for each predictor was taken as the baseline (null) value (w_{+0}). For each term the absolute weight of evidence

(Δw_{+i}) was obtained by subtracting w_{+0} from w_{+i} , and predictors with Δw_{+i} of zero or less have essentially no explanatory power (Burnham & Anderson 2002). All statistical analyses were done using the R PACKAGE (Ver. 2.0.1, Ihaka & Gentleman 1996). Values are presented as mean \pm 1 SEM unless otherwise stated.

Results

We obtained mass and body composition measurements at PP for 26 females and 29 pups in 2002, and for 25 females and 25 pups in 2003 (Table 1). End-lactation measurements were calculated for 24 females and 25 pups in 2002, and 11 females and 22 pups in 2003. In 2003, 14 females were not captured at EL because they ended lactation earlier than expected. However, the average MPPM of these females was not significantly different to that of the females that were re-captured (384.8 ± 12.98 kg and 403.6 ± 18.82 kg, respectively; $t_{18.6} = -0.82$, $P = 0.422$), so we considered that any potential bias that this may have posed for between-year comparisons was negligible.

BODY MASS CHANGES

Females

The most-parsimonious GLM testing for the effect of *age*, *year* and *length* on MPPM included all terms and a *length*year* interaction. Using relative weights of evidence (Δw_{+i}), *year* and *length* were the only factors driving the relationship ($\Delta w_{+year} = 0.741$, $\Delta w_{+length} = 0.743$, $\Delta w_{+age} = 0.000$), demonstrating that females were heavier in 2002. In 2003, shorter females were considerably lighter compared with females of similar length in 2002 (Fig. 1). From predictive model averaging, using all a priori models and keeping *age* and *length* constant, overall MPPM was 12.7% higher in 2002 than in 2003.

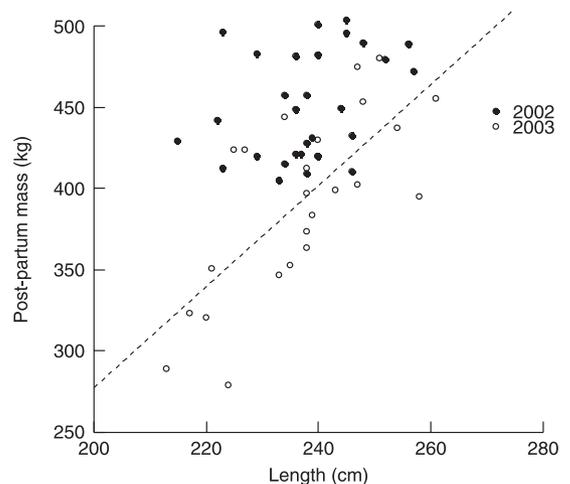


Fig. 1. Relationship between body length and post-partum mass. The dashed line represents the positive relationship for 2003 ($y = 3.12x - 346.4$).

Table 1. Average mass and body composition of Weddell seal females and pups during lactation in 2002 and 2003

	2002						2003					
	Birth	<i>n</i> = 26	Wean	<i>n</i> = 24	Change	<i>n</i> = 24	Birth	<i>n</i> = 25	Wean	<i>n</i> = 11	Change	<i>n</i> = 11
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Females												
Body mass (kg)	450.9	6.13	294.0	6.32	158.9	4.07	393.1	10.94	267.6	10.92	135.9	9.29
Total body lipid (kg)	181.5	3.78	82.2	3.16	100.2	4.17	153.4	6.18	70.1	4.27	93.8	9.87
Total body protein (kg)	62.4	1.31	43.2	1.23	19	1.69	55.5	1.74	43.2	2.28	14.9	2.48
Body lipid percentage	40.2	0.67	31.2	1.09	9.3	1.32	38.9	0.93	28.2	1.55	11.4	2.30
Body protein percentage	13.8	0.19	16.4	0.31	2.6	0.38	14.2	0.27	17.2	0.44	3.2	0.66
Total body gross energy (MJ)	8757	150	4326	119	4466	145	7467	260	3842	179	4106	361
Pups												
	2002						2003					
	Birth	<i>n</i> = 29	Wean	<i>n</i> = 25	Change	<i>n</i> = 25	Birth	<i>n</i> = 25	Wean	<i>n</i> = 22	Change	<i>n</i> = 22
	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM
Body mass (kg)	27.6	0.73	96.8	2.23	69.2	1.97	26.7	0.95	76.5	3.19	49.6	3.27
Total body lipid (kg)	2.4*	0.06	40.5	2.01	48.1	1.99	2.4	0.15	34.7	2.09	32.4	2.12
Total body protein (kg)	6.3*	0.16	12.1	0.32	5.8	0.35	6.1	0.22	11.6	0.44	5.8	0.49
Body lipid percentage	8.6*	–	47.8	1.07	39.2	1.07	8.6	0.49	40.1	1.00	31.3	1.20
Body protein percentage	22.8*	–	11.6	0.30	11.2	0.31	22.8	0.14	13.8	0.29	8.9	0.34
Total body gross energy (MJ)	246*	6	2307	80	2061	78	244	10	1666	91	1432	94

*Values averaged from pup TBW measurements in 2003.

Mass loss rates ranged from 3.9 to 5.9 kg day⁻¹ (4.7 ± 0.12) in 2002, and 2.1–5.1 kg day⁻¹ (4.0 ± 0.27) in 2003. MPPM was largely responsible for differences in mass loss rates, although TBL was also an important factor ($\Delta w_{\text{MPPM}} = 0.769$, $\Delta w_{\text{TBL}} = 0.320$, $\Delta w_{\text{year}} < 0.0$, $\Delta w_{\text{age}} = 0.003$). Therefore, heavier females had higher mass loss rates (Fig. 2). Mass-specific mass loss rates averaged 10.67 ± 0.24 g kg⁻¹ day⁻¹ and 10.38 ± 0.42 g kg⁻¹ day⁻¹ in 2002 and 2003, respectively. Over the entire lactation period, total mass loss ranged from 161 to 245 kg in 2002 and 78 to 206 kg in 2003. This represented 41.5 ± 0.01% of MPPM in 2002 and

38.5 ± 0.02% in 2003. MPPM had the most influence on percentage mass loss ($\Delta w_{\text{MPPM}} = 0.639$) with no *year* or *TBL* effect ($\Delta w_{\text{year}} = 0.0$). Therefore, heavier females lost a higher proportion of body mass over lactation, with no differences between years.

Assimilation

In 2002, pups assimilated 41.9 ± 0.01% (34.1–59.6%) of the mass lost by their mother, and in 2003 pups assimilated 36.9 ± 0.01% (25.8–46.1%). The most-parsimonious model testing for the effect of *age*, *MPPM*, *birth mass (BM)* and *year* on mass transfer efficiency (pup mass gain/female mass loss) only included a *year* effect ($\Delta w_{\text{year}} = 0.394$; $\Delta w_{\text{year}} < 0.0$ for all other terms). Model averaging revealed that mass transfer efficiency was 10.2% higher in 2002 than in 2003.

Pups assimilated 45.7 ± 0.02% (22.4–57.7%) of the energy (MJ) lost by the mothers in 2002, and 40.4 ± 0.03% (28.7–59.2%) in 2003. The *year* term had a strong influence on this proportion ($\Delta w_{\text{year}} = 0.396$), but *MPPM*, *age* and *TBL* had no effect ($\Delta w_{\text{year}} = 0.0$). Model averaging estimated that energy transfer efficiency was 5.4% higher in 2002 than in 2003.

Pups

Average birth mass of pups was 27.6 ± 0.7 kg in 2002, and 26.7 ± 1.0 kg in 2003. The most-parsimonious model testing for the effect of *MPPM*, *TBL*_{MPPM}, *year* and *sex* on average birth mass revealed that *MPPM*

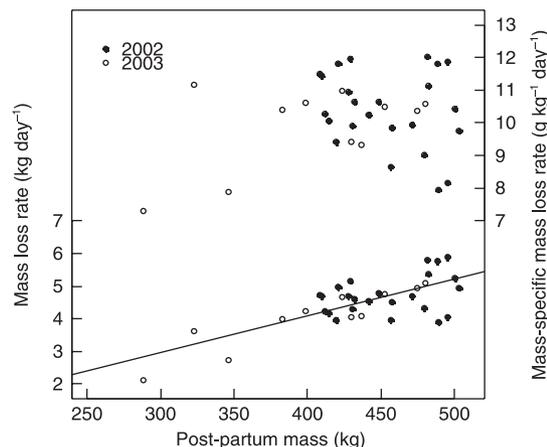


Fig. 2. Daily rate of mass loss and the mass-specific mass loss rate in relation to post-partum mass.

was the most important term in the model ($\Delta w_{+MPPM} = 0.386$, $\Delta w_{+} = 0.0$ for all other terms). However, only 7.6% of the deviance was explained by this model.

Pup mass gain ranged from 1.5 to 2.5 kg day⁻¹ (1.9 ± 0.04) in 2002, and 0.5 to 2.4 kg day⁻¹ (1.6 ± 0.10) in 2003. The most-parsimonious model testing for the effect of *MPPM*, *TBL*_{MPPM}, *sex* and *year* on total mass gain (to EL) included the *MPPM*, *year* and *TBL*_{MPPM} terms, with *MPPM* driving the relationship ($\Delta w_{+MPPM} = 0.720$, $\Delta w_{+year} = 0.002$, $\Delta w_{+TBL} = 0.000$). Thus, larger females produced larger pups (Fig. 3).

BODY COMPOSITION AND ENERGY EXPENDITURE

Females

Post-partum lipid content ranged from 150.5 to 223.6 kg in 2002, representing 32.5–45.7% of female body mass. In 2003, lipid content ranged from 105.3 to 199.3 kg, or 25.7–45.5% of body mass. *MPPM* had only a moderate influence on this proportion ($\Delta w_{+MPPM} = 0.287$), but *year* and *age* had no effect ($\Delta w_{+} = 0.0$); therefore, proportionately all females had similar compositions. Protein content ranged from 54.0 to 77.0 kg, representing 12.2–16.0% of *MPPM* in 2002. In 2003, TBP ranged from 40.4 to 77.2 kg or 12.2–17.9% of *MPPM*. The total body gross energy (TBGE) varied from 7539 to 10 384 MJ in 2002 and 5180 to 9292 MJ in 2003, representing an energy density of 16.9–21.2 MJ kg⁻¹ (19.4 ± 0.22) and 14.6–21.0 MJ kg⁻¹ (19.2 ± 0.60) in 2002 and 2003, respectively.

At EL, *TBL* ranged from 50.5 to 115.6 kg in 2002 and 49.5 to 91.7 kg in 2003, representing 22.9–42.0% and 19.0–33.6% of body mass, respectively. The most-parsimonious GLM testing for the effect of *MPPM*, *TBL*_{MPPM}, *year* and *pup sex* on total lipid loss indicated that *pup sex* was largely responsible for driving the relationship ($\Delta w_{+sex} = 0.385$, $\Delta w_{+} = 0.0$ for all other terms). Mothers with male pups lost 19.6% more lipid on average than those with female pups (male lipid loss = 11.1%; female lipid loss = 9.3%).

Lipid constituted 36.1–92.4% ($54.5 \pm 0.03\%$), and protein 1.1–15.0% ($9.7 \pm 0.01\%$) of the mass lost over lactation in 2002, and mass lost comprised 23.1–70.1% ($57.0 \pm 0.03\%$) lipid and 5.1–18.7% ($9.3 \pm 0.01\%$) protein in 2003. *TBL*_{MPPM} was the only variable that influenced percentage lipid loss over lactation ($\Delta w_{+TBL} = 0.891$, $\Delta w_{+year} = 0.125$, $\Delta w_{+MPPM} < 0.0$).

Pups

Body composition at birth was measured for all pups ($n = 25$) in 2003 and average values applied to pups in 2002 (see Methods; Table 1). For pups in 2002, lipid and protein represented $61.9 \pm 0.01\%$ (48.8–84.0%) and $7.6 \pm 0.005\%$ (1.3–12.1%) of the mass gained, respectively, and lipid constituted $55.3 \pm 0.01\%$ (46.5–69.9%) and protein $9.8 \pm 0.004\%$ (7.2–12.0%) of the mass gained in

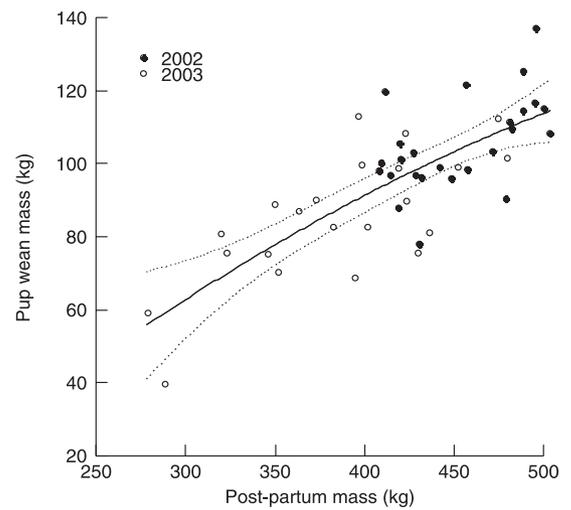


Fig. 3. Relationship between post-partum mass and pup mass at weaning. Broken lines represent the 95% confidence interval of the fitted curve.

2003. The most-parsimonious model testing for the effect of *MPPM*, *TBL*_{MPPM}, *sex* and *year* on *TBL*_{pup} at EL included all variables; however, *MPPM* and *sex* were largely responsible for driving this relationship ($\Delta w_{+MPPM} = 0.735$; $\Delta w_{+sex} = 0.560$, $\Delta w_{+year} = 0.159$, $\Delta w_{+TBL} < 0.0$). Model averaging estimated that females had 4.5% higher lipid content than males at the end of lactation.

LACTATION LENGTH

Despite extrapolating lactation duration for 23 individuals, those females for which the entire duration of lactation was known demonstrated that duration was longer in 2002 (39.8 ± 1.40 days; range = 31–49 days; $n = 13$) than in 2003 (35.4 ± 0.93 days; range = 28–42 days; $n = 19$). However, *year* did not have a large effect ($\Delta w_{+year} = 0.086$), although *MPPM* did ($\Delta w_{+MPPM} = 0.667$). We fitted a smoothed spline function to the relationship between *MPPM* and lactation length (Fig. 4) to illustrate the nonlinear trend in the data. There appeared to be a mass (355 kg) where the relationship changed, so we tested the importance of *MPPM* on lactation length for females above and below this threshold. *MPPM* was an important term for females ≥ 355 kg ($\Delta w_{+MPPM} = 0.757$) but not for females < 355 kg ($\Delta w_{+MPPM} < 0.0$) where lactation length averaged 33 ± 1.4 days. There were two noticeable outliers: ‘P130’ had a longer lactation (41 days) than expected for her mass, while ‘Y4125’ had a shorter one (28 days).

Discussion

Reproductive performance responds to and reflects interactions with the environment, and it is thought to relate to current or recent phenomena (Crocoll 1992). The Southern Ocean is subject to a number of events

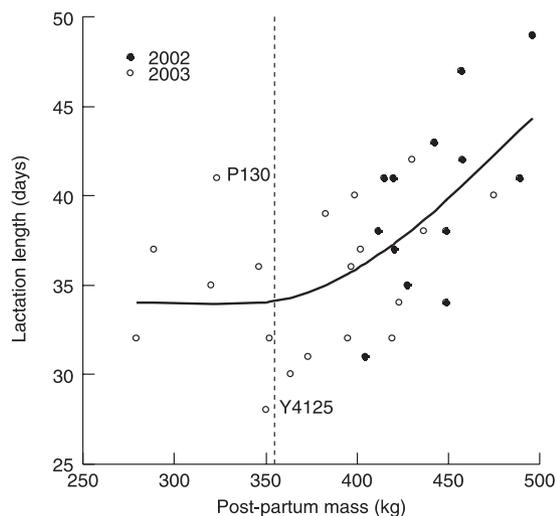


Fig. 4. Relationship between post-partum mass and lactation length. The curve is a smooth spline function fitted to illustrate the trend of the data. The vertical line denotes a suggested minimum mass range (< 355 kg) where a female will limit her lactation length. The linear function of the curve after 355 kg is $y = 0.07x + 6.98$, $r^2 = 0.36$, $P = 0.002$.

that have measurable effects on sea ice extent and ecosystem structure (Nicol *et al.* 2000). For instance, ice thickness was higher in 2003 than in 2002 (Lesser, Lamare & Barker 2004), and this variation can strongly influence phytoplankton production (Seibel & Dierssen 2003) and ultimately the performance of higher trophic level grazers and predators. Therefore, physiological or behavioural patterns in these species might reflect such environmental variation (Le Boeuf & Crocker 2005). As capital breeders, phocid seals rely heavily on foraging success prior to parturition and their resultant body reserves influence reproductive rate and the total amount and rate of energy expenditure to offspring. Thus, the constraints imposed by this strategy for lactation are useful for examining the consequences of environmental variability over a short time span (*c.* 1 year).

Life-history theory predicts that for species in which survival rates are higher for adults than juveniles, fitness is maximized by forgoing reproduction when conditions are unfavourable (Stearns 1992). For a female in poor body condition, the optimal strategy is to allocate resources to self-maintenance rather than reproduction. Although previous studies of Weddell seals have shown variability in reproductive rate (Siniff *et al.* 1977; Testa *et al.* 1990) there is also evidence that females in poor condition will still produce and rear a pup (this study), although the long-term costs remain unknown.

We found that female body mass (and absolute body fat) at parturition differed between the 2 years of study and that this difference influenced lactation length, maternal expenditure, pup mass gain and weaning mass (and by inference, pup survival – McMahon *et al.* 2000; Hall *et al.* 2001). Life-history theory predicts a

trade-off between mass and reproduction when resources are limited, and populations of upper trophic level predators are thought to be limited ultimately by food availability (Testa *et al.* 1991; Croxall 1992), so individuals that encounter different levels of resource availability during their lifetimes should select for a flexible strategy of maternal expenditure (Festa-Bianchet, Gaillard & Jorgensen 1998). The variation in reproductive effort we observed may demonstrate the flexibility in expenditure as a function of female condition and environmental constraints, *i.e.* in ‘good’ years females were able to expend more because the potential cost (loss of future breeding) was lower.

We suggest that the lactation length for Weddell seals at McMurdo Sound is 5–6 weeks, compared with the generally accepted estimation of 6–7 weeks by Tedman & Green (1987). Our estimate agrees with two previous accounts (Stirling 1969; Kaufman, Siniff & Reichle 1975). Although lactation is generally longer for Weddell seals than in other phocids, the duration appears to be highly variable. There was a positive relationship between MPPM and lactation length for larger females (≥ 355 kg), but not for smaller females (< 355 kg). This suggests that there was a minimum lactation time (*c.* 35 days) regardless of how small a female was, but as mass increased (≥ 355 kg) more energy was available for maintenance and allocation resulting in a longer lactation. Therefore, lactation length for smaller seals would be shorter than expected (like in 2003) according to previous estimates.

Newly arriving females were heavier in 2002 than in 2003; however, there were interannual differences in the relationship between length and mass. In 2003, shorter females were lighter compared with their counterparts of the same length in 2002, regardless of age. On the other hand, longer females were the same mass in both years, indicating that the foraging success of shorter seals is more susceptible to environmental variation. If true, quantifying these patterns in smaller females may provide the best ‘ecosystem indicator’ of change within this marine ecosystem.

Eisert *et al.* (2005) found that females fasted within the first 3–4 weeks of lactation but as weaning approached, feeding occurred in 70% of the sample population. However, it is still unclear which individuals (smaller vs. larger) invoke this behaviour during lactation, how much feeding (net gain) occurs, and whether feeding depends on the success of overwinter foraging. Our results appear to indicate that at-sea differences prior to lactation are evident in MPPM, but differences in expenditure throughout lactation could be still influenced by foraging. This may be particularly important for smaller individuals if some can achieve higher mass and energy transfer and longer lactation periods than expected. Consequently, records of longer lactations (53 ± 5 days, Thomas & DeMaster 1983) may be the result of females foraging and being able to remain with their pups longer. Nevertheless, females must have a considerable net gain from foraging before they can deliver any extra energy to their pup (Boyd 1998). Presumably

foraging would have to occur in the immediate vicinity where the prey source was abundant; otherwise, increased searching may influence available suckling time. High prey abundance is perhaps unlikely in McMurdo Sound where seal densities are high (Stirling 1969) and the available foraging area (per individual) is small (Hindell *et al.* 2002). Furthermore, Testa, Hill & Siniff (1989) inferred feeding from exceptionally high mass transfer efficiency rates, and although there was a negative relationship between efficiency and MPPM, the variation explained by MPPM was small ($r^2 = 0.099$). We found only a narrow range of efficiency (36.9–59.6%), so we were unable to predict female foraging in either year. However, recent fatty acid composition analysis has indicated that some feeding did occur within smaller individuals (K.E. Wheatley unpublished data). Furthermore, the outliers in the MPPM–lactation length relationship (Fig. 4) may provide more insight into probable feeding. Seal 'P130' was small in 2003 yet had a relatively long lactation period (41 days) for her size, and 'Y4125' was larger but departed earlier than expected (Fig. 4). Unfortunately, we were unable to collect EL data for Y4125; however, P130 had higher-than-average per cent mass loss (45.5 vs. 37.8%), and a higher-than-average energy transfer efficiency (45.0 vs. 40.4%). It may be that P130 foraged during lactation, but also invested more in her pup by staying longer at a possible cost to her own condition and survival.

Testa *et al.* (1989) found a weak negative relationship with MPPM and mass transfer efficiency from a pooled three-year data set. Our longitudinal data revealed that mass and energy transfer efficiency differed between years but were not related to MPPM or TBL. In 2003 vs. 2002, females had a 10.2 and 5.4% lower rate of mass and energy transfer, respectively. If females foraged successfully during lactation in this poorer-resource year, one might predict a higher rate of transfer efficiency between mother and pup. However, our data revealed the opposite – in 2003 expenditure was lower. This suggests that females actively searched for food and expended more energy, but were unsuccessful in prey acquisition.

Although MPPM had a moderate effect on total body lipid (TBL) at post-parturition, only 2.6% of the deviance was explained by this model. Therefore, although heavier females had more lipid and more lean tissue than lighter ones, the proportion of lipid to body mass was similar in all individuals, even at the end of lactation. Females with male pups lost proportionately more lipid than those with female pups; however, only 15.0% of the deviance was explained by this model. Contrary to this, TBL of female pups at weaning was higher than that of males. Biuw (2003) found that post-weaned male elephant seal pups relied more on lipid metabolism for their energetic needs than females. Because Weddell seal pups swim and dive during the lactation period, their energetic demands are higher than those of most other species. Our data suggest that differential resource use by pups may occur during lactation. We suggest that males may be predisposed to

use more lipid, so although they receive more lipid during lactation, they have less at the end of lactation relative to females.

We found no differences in pup birth mass between the sexes or between years, and only weak evidence for a relationship with MPPM. This indicates that there was no differential expenditure during gestation between differently sized females. This contrasts with other studies where birth mass was correlated to maternal mass (Costa *et al.* 1986; Bowen *et al.* 1994). Total mass loss as a percentage of initial MPPM was similar between years for all females with known weaning dates (2002: 39.9%, 2003: 37.8%). This is comparable with that previously reported for Weddell seals (37%, Hill 1987), and to the 34–42% mass loss of elephant seals (Arnbom, Fedak & Boyd 1997; Carlini *et al.* 1997; Crocker *et al.* 2001b), suggesting that there is a relatively fixed proportion of MPPM (*c.* 60%) to which an individual female can deplete her reserves before terminating lactation. As a result, pups of larger females acquired relatively more from their mother's energy stores and for a longer period of time.

Our results demonstrate differences in maternal mass and expenditure during lactation for a capital breeder that probably reflect environmental variability during the period of prey acquisition, and that these effects were more marked in smaller individuals. Smaller individuals did not increase energy expenditure to reconcile this disparity, resulting in reduced pup mass and condition at weaning. This is an important finding for general life-history theory in long-lived mammals in terms of providing evidence for reproductive flexibility in a highly variable and challenging environment. We suggest that the trade-off between long-term survival in breeding females and the success of their offspring is contingent on individual size, and this is complicated by the possibility of feeding during lactation to offset nutritional constraints imposed during poor-resource years.

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