Interannual and individual variation in milk composition of New Zealand sea lions (*Phocarctos hookeri*)

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In this study 308 milk samples were collected and analyzed from 181 individual female New Zealand sea lions (NZ sea lions; *Phocarctos hookeri*) breeding on Enderby Island (Auckland Islands). Samples were collected from the 1st part of early lactation (January and February) over a period of 7 years (1997, 1999–2003, and 2005). The effect of year, month, and maternal characteristics (body mass, body condition index [BCI], and age class) on the composition of milk was evaluated using a mixed model for repeated measures. The gross composition ($\pm$ *SD*) of the milk was lipid (21.3% $\pm$ 8.1%), protein (9.4% $\pm$ 2.4%), water (67.9% $\pm$ 8.8%), ash (0.48% $\pm$ 0.06%), and energy content (10.3 $\pm$ 3.2 kJ/g). Overall, the quality of milk of the NZ sea lions in this study was relatively lower in solids and fats than that of other pinnipeds and, in particular, other sea lion species. There were significant effects of year and month on the concentration of lipids in milk, and of year and maternal age class on maternal body mass and BCI. There were significant relationships between various maternal characteristics and milk composition. Thus, the concentration of milk lipids was significantly correlated with maternal BCI, body mass, and pup age. Given that NZ sea lions are a nationally critical species in decline, the relationship between the temporal (yearly and monthly) variations in milk composition, maternal body mass, reproductive success, and changes in food supply in relation to natural perturbations or fisheries resource competition warrants further investigation to disentangle this relationship and implement appropriate management initiatives.

Key words: energy, lipid, milk, New Zealand sea lions, *Phocarctos hookeri*, protein

The survival of mammalian offspring from early to juvenile stages has major implications for natural selection and population dynamics (Hayssen 1993; Lee et al. 1991). Prior to weaning and during early development stage, mammalian offspring rely entirely or almost entirely on the mother's milk

to survive, and therefore are influenced by maternal nutrition and energy allocation (McAdam and Boutin 2003; Rogowitz and McClure 1995). In addition, maternal nutrition in mammals plays a determinant role in offspring survival after weaning (Gaillard et al. 2000; Kerr et al. 2007; Ylönen et al. 2004). For instance, in large herbivores, higher food quality and quantity improved offspring survival (Rognmo et al. 1983), likely due to enhanced milk quality (Wilson and Hirst 1977).

Lactation is the most energetically demanding stage in a mammal's life cycle, and pinnipeds are no exception (Costa 1991b; Gales et al. 1996). Pinnipeds, true seals (family Phocidae) and eared seals (family Otariidae), secrete milk with a higher fat concentration than that of most terrestrial mammals (Costa 1991b; Oftedal 1988) and other marine mammals including dolphins (Pervaiz and Brew 1986; Pilson and Waller 1970) and whales (Costa 1991a; Gregory et al. 1955). Otariids, sea lions and fur seals, produce lipid-rich, energy-dense milk that enables their pups to deposit blubber as an insulating thermoregulatory layer and as a fat energy reserve to sustain them while the mothers are foraging at sea (Costa 1991b, 1993). Phocids generally fast for the duration of a short lactation period during which milk is produced from stored fat (capital breeders). In contrast, otariids lactate for a much longer period during which they alternate periods ashore provisioning their pup with periods of foraging at sea (income breeders). Otariid females rely on energy gained during foraging trips to produce their milk (Boness et al. 1994; Bonner 1984; Schulz and Bowen 2005).

Although the gross milk composition of many species of otariids has been reported, detailed studies of milk chemistry are lacking for many species (but see Oftedal and Iverson 1995; Schulz and Bowen 2004). It is likely that several factors are associated with the variation in milk composition, including a complex relationship with the duration of lactation (Costa 1991b). For example, changes in milk composition throughout lactation (Arnould and Boyd 1995a) and in relation to the maternal attendance pattern (Arnould and Boyd 1995b) have been reported. However, the influence of other factors such as maternal body condition, maternal age, and offspring age, which may potentially influence the composition of milk, have not been investigated in detail.

The New Zealand sea lion (NZ sea lion; *Phocarctos hookeri*) is one of the rarest sea lion species (Campbell et al. 2006; Geschke and Chilvers 2009). Following parturition (mean pupping date 26–27 December), lactating females spend more than a week ashore (average perinatal period 8.6 days) before their 1st postpartum foraging trip (Chilvers et al. 2006a). After the perinatal period, lactating NZ sea lions alternate between foraging at sea (average foraging trip duration 2.2 days) and attend their pups ashore on average for 1.3 days (Chilvers et al. 2006b). Their lactation period is thought to last 10 months (Cawthorn 1990). In recent years, considerable advances have been made in our understanding of the growth rates of NZ sea lion pups (Chilvers et al. 2006a, 2009) and attendance patterns (Chilvers et al. 2005, 2006a) and diving–foraging patterns of

sea lion females during lactation (Chilvers 2008; Chilvers and Wilkinson 2009; Chilvers et al. 2005, 2006b). These advances have assisted in the description of the maternal strategies of NZ sea lions. Nevertheless, the composition of their milk and hence the factors that affect milk composition are still poorly understood. Thus, the relationships between the frequency of pup attendance, the foraging and diving behavior of the NZ sea lion females, and their milk production are still unknown. The objectives of this study were to determine the gross chemical composition of NZ sea lion milk; to study the variation in milk composition associated with characteristics of the female such as age, body mass, body condition, and the age of the offspring; and to investigate the temporal changes in milk composition from January to February over 7 breeding seasons and their relationship to the duration of maternal foraging trips preceding milk sampling and duration of haul-out period at the completion of the foraging trip to milk sampling.

MATERIALS AND METHODS

Study site, collection of samples, and animals.—This study was conducted at Sandy Bay, Enderby Island, the Auckland Islands (50°30′S, 166°47′E; Fig. 1), on lactating NZ sea lions
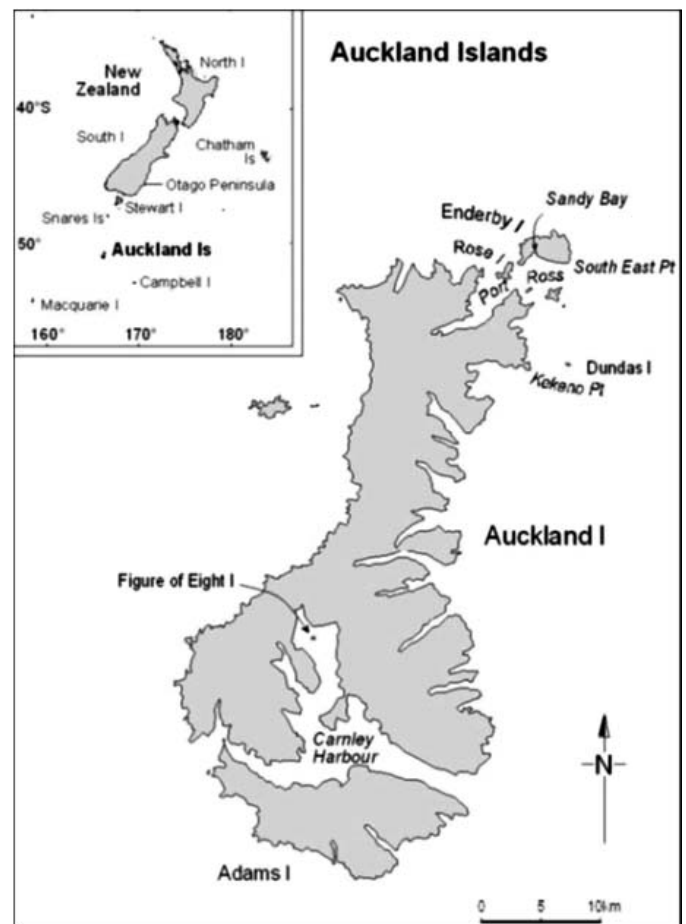

FIG. 1.—Map of New Zealand and the Auckland Islands showing the breeding locations for New Zealand sea lions (*Phocarctos hookeri*) at Enderby Island, Dundas Island, and Figure of Eight Island.

during the 1st part of early lactation (January and February) over 7 austral summer seasons, 1997, 1999–2003, and 2005. Early lactation is considered as the time between partiturition and midlactation. The present study covered the 1st part of early lactation. Between 300 and 400 pups are typically born per season at Sandy Bay, Enderby Island, and it is the 2nd largest breeding colony of the species (representing ∼19% of the entire pup production—Chilvers et al. 2007). The Sandy Bay colony was monitored and surveyed daily during the pupping period, where we recorded the parturition dates (2002–2005, $n = 89$) and sex of pup (1997–2005, $n = 46$) of study females. In January 2000 a total of 135 females were hot-iron branded (Wilkinson et al. 2011) and some of these females were the study animals from that season forward (Childerhouse et al. 2010). Females that had not been tagged at birth, and thus were of unknown age, were aged from sections taken from the 1st postcanine tooth (Childerhouse et al. 2004). Females were captured, handled, and anesthetized as described in Chilvers et al. (2005) and held independent of their pups for the duration of these procedures (15–20 min). Female NZ sea lions were allowed a minimum of 3 h on shore before capture during which time previous observations have established that all the pups had suckled, thus all milk samples were collected after the pup had suckled at least once. Mammary glands were not completely evacuated, thus a representative milk sample between 5 and 30 ml was collected, from 1 or more teats either by manual expression or using a vacuum pump (60-ml plastic syringe). The milk samples stood for 2–6 h at ambient temperature (5–10°C) to let the sand settle to the bottom. Thereafter, the milk was subsampled into 2-ml cryovials and stored in liquid nitrogen (–196°C).

Analytical methods.—The milk fat, protein, and total solids were determined by Fourier transform infrared spectroscopy with a Milkoscan FT 120 (Foss electric A/S, Hillerod, Denmark). The Milkoscan FT 120 was calibrated for fat, protein, and total solids with reference methods for milk analysis as described in Riet-Sapriza et al. (2009). The repeatability and reliability of the results obtained with the calibrated Milkoscan FT 120 were comparable with those obtained using standard methods (Riet-Sapriza et al. 2009). We employed the Roese–Gottlieb method for fat (International Dairy Federation 1987a, 1996), Kjeldahl method for protein (International Dairy Federation 2001), and gravimetric method for total solids (Boon 1979; International Dairy Federation 1987b; McDowell 1972). Milk water content was calculated as 100% – total solids percent of the milk, whereas gross energy content (kJ/g) was calculated as described by Perrin (1958). To test the reliability of the procedure for subsampling the milk in the field, 3 aliquots from each of 15 different females were analyzed (gross chemical analysis for fat, protein, and total solids with the Milkoscan FT 120) and no significant differences were found between subsamples (Riet-Sapriza 2007). Milk samples ($n = 25$), 5 for each year from 1999 to 2003, were analyzed for minerals (Ca, K, Mg, Na, and P) by elemental analysis using inductively coupled plasma optical emission spectrometry (AOAC International 2000).

Maternal age class.—Age and parity were used as criteria to pool breeding females into 3 age classes: primiparous mother (3–7 years old), prime age mother (8–13 years old), and old mother (14–26 years old). Animals were parous from age 4 and parity peaked between the age of 8 and 13 years (Chilvers et al. 2010). Age of last reproduction was suggested to be 15–17 years; however, some females reproduce beyond the age of 20 (Chilvers et al. 2010).

Maternal body condition index.—Body condition of lactating females was estimated using a body condition index (BCI) defined by Guinet et al. (1998). The following equation: predicted body weight = 1.51 × (body length) − 157.1, was obtained from the significant regression ($r^2 = 0.55$, $F_{1,435} = 529.25$, $P = 0.001$) between the body weight and length of individual NZ sea lion females ($n = 435$) than that described for milk samples. The data set included those females from which milk samples were collected, along with additional females at Sandy Bay (Enderby Island, Auckland Islands) that formed part of another study (Childerhouse 2007).

Maternal attendance pattern.—The maternal duration of the preceding foraging trip and the time from haul-out at the completion of the foraging trip to milk sampling at Sandy Bay was determined by monitoring 65 lactating females were fitted with very-high-frequency transmitters (Sirtrack, Havelock North, New Zealand; Table 1). To locate the sea lions by very-high-frequency transmitters, Sandy Bay was scanned manually with a receiver 3 times (0900 h, 1200 h, and 1800 h) each day; and with an automatic scanning receiver and data logger (model R2000; Advanced Telemetry Systems, Inc., Isanti, Minnesota).

All animal-handling and sample-collection procedures followed guidelines approved by the American Society of Mammalogists (Sikes et al. 2011) and by the Department of Conservation (New Zealand) Animal Ethics Committee.

Statistical analysis.—Normality was tested by plotting residuals against predicted values and Levene's test (Levene 1960) was used to determine equality of variance. Repeated measures for milk components (lipid, protein, and energy content) and maternal body condition (BCI) and body mass were analyzed with a mixed model for repeated measures (PROC MIXED procedure; SAS Institute Inc., Cary, North Carolina [Littell et al. 1998]). The mixed model included the fixed effects of year, month (nested within year), and age class and the random effect of animal. Using the Akaike's information criterion, a compound symmetry error structure was determined as the most appropriate residual covariance structure for repeated measures over time within animals. Other error structures evaluated were unstructured, Toeplitz, and autoregressive of order 1. When variances were not homogenous among levels of fixed effects a heterogeneous variance of the residual errors was assumed in the mixed model. Least-squares means (LSMs), their standard errors, and their 95% confidence intervals of dependent variables for each year of sampling were obtained from the mixed model and used for multiple mean comparisons using a *t*-test with a Bonferroni adjustment. Significant differences between years

TABLE 1.—The number of lactating New Zealand sea lions (*Phocarctos hookeri*) from the 1st part of early lactation at Enderby Island, Auckland Islands, sampled either once or twice in early lactation over 7 seasons between 1997 and 2005; the number of milk samples analyzed; the number of females for which age was known (Aged), that were fitted with very-high-frequency tags (VHF), for which body condition index was calculated (BCI), and for which body mass was recorded (Body mass); and the number of pups where age was recorded in each of the 7 years of the study (Pups aged).

| | | No. females with milk sampled | | | No. females | | | | |
Year	n	Once	Twice	Milk samples (n)	Aged	VHF	BCI	Body mass	Pup aged (n)
1997	32	25	7	39	4	24	24	26	—
1999	40	40	—	40	37	—	31	31	—
2000	73	71	2	75	73	—	56	56	—
2001	52	52	—	52	51	—	49	49	—
2002	22	11	11	33	25	12	31	32	23
2003	30	21	9	39	39	21	38	38	39
2005	21	12	9	30	28	8	28	28	30
Total	270	232	29	308	257	65	257	260	92

were declared when $P < 0.05$. The effects of maternal BCI and body mass, pup age, duration of the preceding foraging trip, and time from haul-out to milk sampling on the concentration of lipid and protein and energy content in milk were evaluated using the mixed model as described above including each of these factors as a covariable one at a time. Pearson correlations (r) between milk components (lipid, protein, and energy content) and BCI, maternal body mass, pup age, and attendance pattern were determined (CORR procedure; SAS Institute Inc.). Correlations were considered to be significant if $P < 0.05$.

Estimates of repeatability for milk fat, protein, and energy content measured on the same animal were estimated with the same mixed model using a number of females that were captured on 2 or more occasions during the period of this study (females, $n = 33$; milk samples, $n = 82$). Repeatability (rep) was calculated as rep $= \sigma^2_a/(\sigma^2_a + \sigma^2_e)$, where σ^2_a is the variance between animals and σ^2_e is the variance within animal (West et al. 2007). This definition of repeatability measures the proportion of the total variance that is due to the genetic additive effects plus the permanent environmental effects that the animals acquire during their lives (Falconer and Mackay 1996).

RESULTS

Descriptive statistics.—The number of milk samples, females, and offspring that were included in this study are presented in Table 1. A total of 308 milk samples were collected from 213 identified NZ sea lion females over a period of 7 years, with 29 females sampled twice in the same year and with 37 females that were sampled 2–4 times in different years. The mean ($\pm$ *SD*) values of the components measured in the milk, maternal characteristics, pup age, and attendance pattern estimated from cross-sectional data are shown in Tables 2–4. The sum of all the components measured in the milk (fat + protein + minerals + the estimated water content) accounted for a mean of 98.5% $\pm$ 5.5% ($n = 308$) of the milk mass,

indicating that the milk contained only a small amount of carbohydrates. Consequently, milk samples in this study were not analyzed for carbohydrates. There was more than a 7-fold range in the values for fat content and a 6-fold range for protein content (Table 2). On a fat-free basis (skim milk), the range of protein concentrations was approximately 6-fold (Table 4). The molar concentrations of the ions are presented in Table 4, and the mean ratio of K^+ to Na^+ was 0.89. The repeatability of the concentration of fat, protein, and energy in milk of NZ sea lions collected from the same individual either twice in 1 year (within season) or in more than 1 year (between years) ranged between rep $= 0.25$ and rep $= 0.31$.

Milk lipid.—The fixed effects of year and month were significant in the repeated-measures mixed model for milk fat ($F_{6,281} = 11.41$, $P < 0.001$; $F_{7,284} = 2.91$, $P = 0.006$, respectively); whereas maternal age class did not have a significant effect on milk fat concentration ($F_{3,281} = 2.55$, $P = 0.056$). The interannual variation in milk concentration is shown in Fig. 2a. Lactating females produced milk with significantly lower milk fat concentration in January (20.5%, 18.9–22.2%, LSM), than in February (22.9%, 21.5–24.3%, LSM, $t_{284} = -2.18$, $P = 0.029$). Maternal BCI ($F_{1,242} = 12.16$, $P < 0.001$) and maternal body mass ($F_{1,245} = 9.57$, $P = 0.002$)

TABLE 2.—Mean gross chemical composition of whole milk of New Zealand sea lions (*Phocarctos hookeri*) collected in the 1st part of early lactation over 7 seasons between 1997 and 2005 at the breeding site of Sandy Bay, Enderby Island, Auckland Islands.

	$\bar{X}$	SD	n	Range
Lipid (%)	21.3	8.1	308	8.3–64.8
Protein (%)	9.2	2.4	307	3.2–20.8
Water (%)	67.9	8.8	308	26.0–88.4
Total solids (%)	32.1	8.8	308	11.6–74.0
Gross energy (kJ/g)	10.3	3.2	308	4.8–22.2
Ash (%)	0.48	0.06	25	0.39–0.59
Calcium (mg/kg)	764.1	161.7	25	520–1,090
Potassium (mg/kg)	1,530.4	395.2	25	875–2,430
Magnesium (mg/kg)	132.3	29.8	25	75.9–156
Sodium (mg/kg)	1,015.1	206.6	25	668–1,430
Phosphorus (mg/kg)	1,326.5	223.9	25	962–1,760

TABLE 3.—Descriptive statistics for maternal characteristics, pup age, and maternal attendance pattern (duration of maternal foraging trips preceding milk sampling and duration from haul-out to milk sampling) of New Zealand sea lions (*Phocarctos hookeri*) from the 1st part of early lactation at Enderby Island, Auckland Islands, for 7 seasons between 1997 and 2005. Sample sizes, mean values, standard deviations, and maximum and minimum values are given.

Traits	n	$\bar{X}$	SD	Minimum	Maximum
Maternal body condition index	257	0.19	10.20	−25.46	38.78
Maternal body mass (kg)	260	112.6	15.60	76.5	162.2
Maternal body length (cm)	257	177.9	7.30	157.0	195.0
Maternal age (years)	257	10.9	4.00	4	26
Pup age (days)	89	32.7	14.44	5	61
Duration of haul-out (h)	045	12.9	12.00	0.42	56.64
Duration of foraging trips (h)	041	41.7	24.70	6.48	96.0

had a significant effect on milk fat concentration, whereas pup age ($F_{1,34} = 0.93$, $P = 0.34$), duration of maternal foraging trip preceding milk sampling ($F_{1,2} = 1.94$, $P = 0.29$), and time from haul-out to milk sampling ($F_{1,1} = 1.56$, $P = 0.43$) did not.

Milk protein.—There was a significant effect of year of sampling on the concentration of protein in the milk ($F_{6,242} = 6.35$, $P < 0.001$; Fig. 2b). Month and age class did not significantly affect milk protein concentration ($F_{7,280} = 2.01$, $P = 0.054$; $F_{3,280} = 1.04$, $P = 0.376$, respectively). Interannual variation in milk protein concentration is shown in Fig. 2b. There was a significant effect of maternal BCI ($F_{6,241} = 6.23$, $P = 0.01$) and maternal body mass ($F_{1,244} = 7.50$, $P = 0.007$) on the concentration of protein in milk. Pup age ($F_{1,34} = 0.04$, $P = 0.85$), duration of maternal foraging trip preceding milk sampling ($F_{1,2} = 2.42$, $P = 0.26$), and time from haul-out to milk sampling ($F_{1,1} = 0.27$, $P = 0.69$) did not have significant effect in the repeated-measures mixed model for milk protein.

Milk energy content.—As with milk fat concentration, year ($F_{6,281} = 10.97$, $P < 0.001$) and month ($F_{7,281} = 3.20$, $P = 0.003$) had significant effects in the repeated-measures mixed model for milk energy content. The maternal age class variable did not significantly affect milk energy content ($F_{3,281} = 2.41$, $P = 0.068$). Interannual variation in milk protein concentration is shown in Fig. 2c. Milk had significantly more energy content ($t_{35} = -2.16$, $P = 0.038$) in February (11.2 kJ/g, 10.6–11.7 kJ/g, LSM) than in January (10.2 kJ/g, 9.4–10.9 kJ/g, LSM). The effect of BCI ($F_{1,242} = 14.46$, $P = 0.002$) and maternal body

TABLE 4.—Calculated concentrations of protein (%) and major cations (mM) in skim milk of New Zealand sea lions (*Phocarctos hookeri*) from the 1st part of early lactation period collected over 7 seasons between 1997 and 2005 at Sandy Bay, Enderby Island, Auckland Islands.

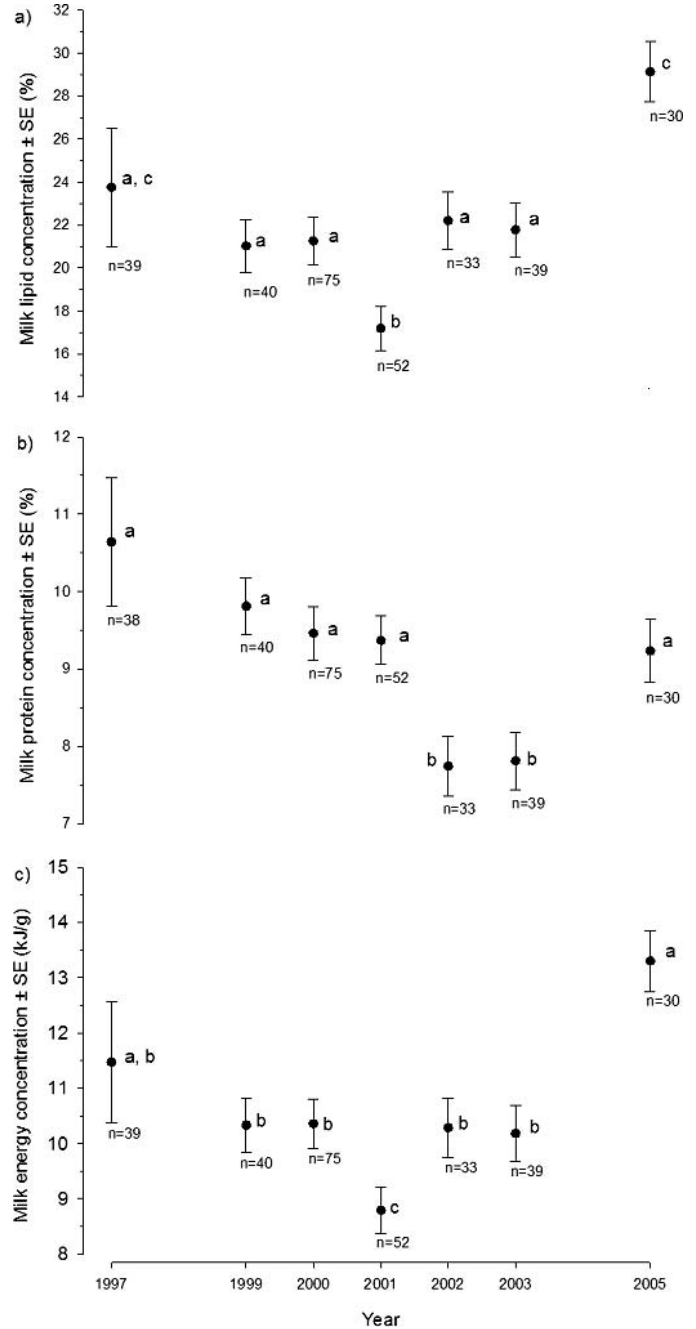|	$\bar{X}$	SD	n	Range
Protein in skim milk (%)	11.9	3.1	303	3.6–21.1
Calcium (mM)	22.85	6.12	25	14.55–35.55
Potassium (mM)	46.17	10.91	25	24.66–70.50
Magnesium (mM)	6.68	1.83	25	3.59–10.00
Sodium (mM)	51.66	8.77	25	31.98–83.37

FIG. 2.—Least-squares means ($\pm$ *SE*) of the a) milk lipid concentration (%), b) milk protein concentration (%), and c) milk energy content (kJ/g) of New Zealand sea lions (*Phocarctos hookeri*) from the 1st part of early lactation collected over 7 summers between 1997 and 2005 at Sandy Bay, Enderby Island, Auckland Islands. Means with different letters are significantly different ($P < 0.05$).

mass ($F_{1,245} = 11.93$, $P < 0.001$) on the energy content in milk was significant. Pup age ($F_{1,34} = 0.91$, $P = 0.35$), duration of maternal foraging trip preceding milk sampling ($F_{1,2} = 1.76$, $P = 0.32$), and time from haul-out to milk sampling ($F_{1,1} = 1.32$, $P = 0.46$) did not have a significant effect.

Maternal body condition.—The fixed effect maternal age class was significant ($F_{3,13} = 3.60$, $P = 0.04$) in the repeated-
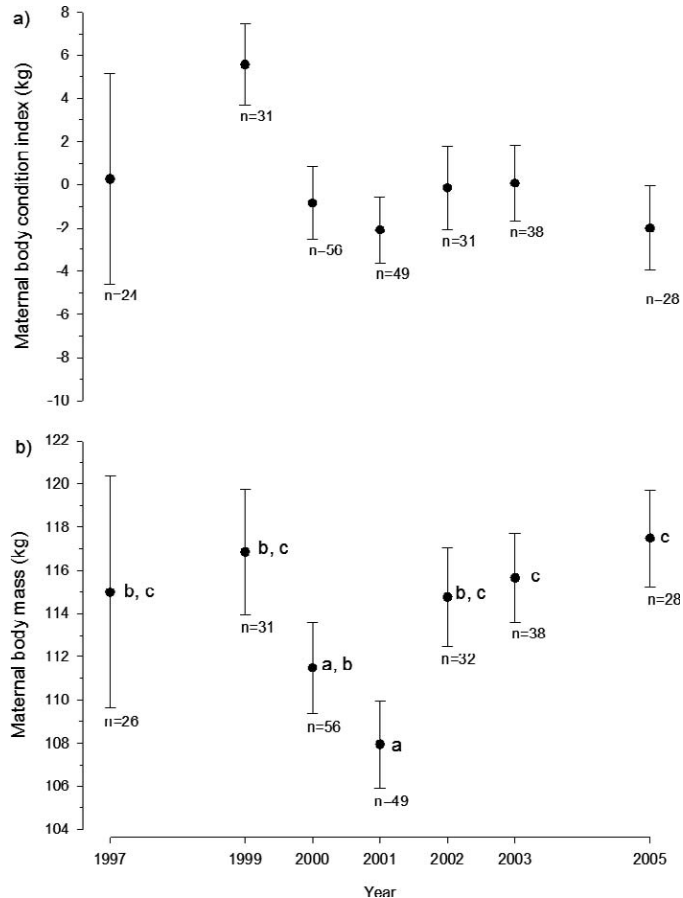
FIG. 3.—Least-squares means ($\pm$ *SE*) of a) maternal body mass (kg) and b) maternal body condition index of lactating New Zealand sea lions (*Phocarctos hookeri*) from the 1st part of early lactation during 7 years between 1997 and 2005 at Sandy Bay, Enderby Island, Auckland islands. Means with different letters are significantly different ($P < 0.05$).

FIG. 4.—Pup age (days) and a) milk lipid concentration (%) and b) milk protein concentration (%) of lactating New Zealand sea lions (*Phocarctos hookeri*) from the 1st part of early lactation between 2002 and 2005 at Sandy Bay, Enderby Island, Auckland Islands.

measure mixed model for maternal BCI, whereas the fixed effects of year and month of sampling were not significant ($F_{6,35} = 2.03$, $P = 0.088$; $F_{7,23} = 0.62$, $P = 0.73$, respectively). The older NZ sea lion mother age class (2.06, -1.22–5.33, LSM) had significantly better body condition than did primiparous mothers (-4.28, -8.26–0.29, LSM, $t_{13} = 3.01$, $P < 0.01$), whereas prime-age mothers (-0.45, -3.24–2.33, LSM) did not have a significantly better body condition than primiparous mothers (LSM, $P > 0.05$).

Maternal body mass.—Year of sampling ($F_{6,36} = 4.42$, $P = 0.002$) and maternal age class ($F_{3,14} = 5.63$, $P = 0.01$) were significant in the repeated-measure mixed model for maternal body mass. The fixed effect of month of sampling was not a significant effect ($F_{7,23} = 0.69$, $P = 0.68$). In 1999, 2002, 2003, and 2005 females were significantly heavier than in 2001 (LSM, $P < 0.05$) but mothers were not significantly heavier in 2000 than in 2001 (LSM, $P > 0.05$; Fig. 3b). Lactating sea lions were significantly lighter in 2000 than in 2003 (LSM, $t_{36} = -2.24$, $P = 0.04$) and 2005 (LSM, $t_{36} = -2.24$, $P = 0.008$; Fig. 3b). Older sea lion mothers (117.0 kg, 114.9–124.1 kg, LSM) were significantly heavier than primiparous mothers
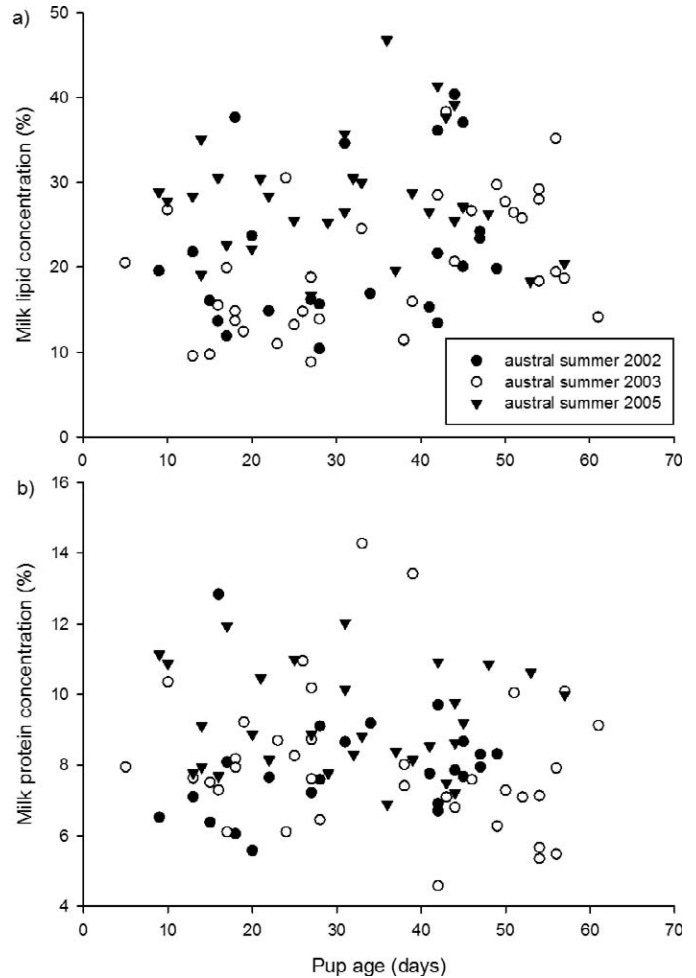
(107.9 kg, 97.7–108.8 kg, LSM, $t_{14} = 3.69$, $P = 0.002$) and prime-age mothers (112.4 kg, 108.1–115.7 kg, LSM, $t_{14} = 2.57$, $P = 0.02$), whereas prime-age mothers were significantly heavier than primiparaous mothers (LSM, $t_{14} = 2.20$, $P = 0.04$).

Correlations with milk components.—The correlations between milk lipid concentration and BCI ($r = 0.19$, $n = 257$), maternal body mass ($r = 0.20$, $n = 260$), and pup age ($r = 0.23$, $n = 89$; Fig. 4) were positive and significant (all $P < 0.05$); whereas the correlations between milk components and the duration of the preceding foraging trip ($r = 0.01$, $n = 31$) and time from haul-out to milk sampling ($r = 0.23$, $n = 45$) were not significant (all $P > 0.05$; Table 5). BCI ($r = 0.16$, $n = 259$) and maternal body mass ($r = 0.17$, $n = 259$) were significantly correlated with protein concentration in whole milk (all $P < 0.05$; Table 5).

DISCUSSION

The solids concentration of milk from NZ sea lions reported here is relatively low in comparison to that of other pinnipeds

TABLE 5.—Correlation coefficients among maternal body condition index (BCI), maternal body mass (kg), pup age (days), maternal attendance pattern (i.e., time ashore and time at sea [h]), and milk components (lipid [%], protein in whole milk [%], and energy content [kJ/g]) of New Zealand sea lions (*Phocarctos hookeri*) from the 1st part of early lactation at Enderby Island, Auckland Islands, for 7 years between 1997 and 2005. *P*-values with an asterisk (*) are significant at $P < 0.05$.

	Lipid (%)			Protein (%)			Energy content (kJ/g)		
	r	*n*	*P*	*r*	*n*	*P*	*r*	*n*	*P*
BCI	0.19	257	0.002*	0.16	259	0.008*	0.22	257	<0.05*
Body mass (kg)	0.20	260	0.001*	0.17	259	0.005*	0.22	260	<0.05*
Pup age (days)	0.23	89	0.029*	−0.09	89	0.410	0.22	89	0.038*
Time ashore (h)	−0.15	45	0.320	−0.29	44	0.056	−0.20	45	0.190
Time at sea (h)	0.01	31	0.940	−0.18	31	0.320	−0.02	31	0.940

and, in particular, other sea lion species. This finding suggests that NZ sea lions may have a different maternal care strategy than other otariids. In addition, milk composition varied significantly with year and for several maternal characteristics. Thus, we hypothesized that the variation in milk composition may reflect the diet and hence the foraging strategy of lactating female NZ sea lions in the Auckland Islands area.

The mean milk lipid concentration during the 1st part of early lactation in NZ sea lions is one of the lowest reported for any otariid (Table 6). In contrast, the mean and range of protein concentrations are comparable to those of other species of otariid (Tables 2 and 6). The range (3.2–20.8%; Table 2) of whole milk protein concentrations in the milk of NZ sea lions was greater than that reported in early lactation for Australian fur seals (*Arctocephalus pusillus doriferus*; range 6.5–16.2%; Table 6— [Arnould and Hindell 1999]). However, the average value for milk protein concentration (8.6%; Table 6) for California sea lions (*Zalophus californianus*) during early lactation (Oftedal et al. 1987b) is similar to that reported here (Table 2). Furthermore, the lipid content reported here is lower than that of fur seal milk (Table 6).

Milk samples in the present study were not analyzed for carbohydrates but the concentrations of fat, protein, and minerals in the milk were sufficient to account for 98.5% of the solids in the milk as determined gravimetrically. Because lactose and other carbohydrates are in low concentration in pinniped milk (Arnould and Boyd 1995a; Dosako et al. 1983; Peaker 1977; Urashima et al. 2001), ions such as K^+, Na^+, and

Cl^- make a greater contribution to the osmotic pressure of the milk (Peaker 1978) than occurs in milk of terrestrial species. Thus, the concentrations of K^+ (1,530 mg/kg) and Na^+ (1,015 mg/kg) are high, and similar to those reported in other pinniped species (Dosako et al. 1983; Le Boeuf and Ortiz 1977; Riedman and Ortiz 1979; Trillmich and Lechner 1986; Webb et al. 1984; Table 2). The mean molar concentrations of K^+ and Na^+ in the skim milk were 46 and 52 mM (Table 3), respectively, which, together with associated anions, could account for up to approximately 200 mOsm of osmotically active solutes in the milk. There would also be some contribution from the Ca^{++} and Mg^{++} that are not bound to proteins. Although this is substantial, it appears there is still a shortfall from the expected osmolality of approximately 280–300 mOsm, but solutes that contribute to the balance of the osmotic pressure are unknown.

In many terrestrial mammals, milk contains a molar ratio of K^+ to Na^+ of approximately 3:1, which is similar to that of intracellular fluids (Peaker 1977). A lower ratio suggests that there is substantial leakage across the glandular epithelium through paracellular pathways (Peaker 1977, 1978). The K^+:Na^+ ratio in the present study was 0.89:1, which is similar to that for California sea lions and northern fur seals (*Callorhinus ursinus*—Dosako et al. 1983). The coefficient of variation for sodium concentration was 17%, which is lower than that for potassium (23%), calcium (27%), and magnesium (27%), indicating that the variance of sodium concentration

TABLE 6.—Mean (± *SD* when available) lipid and protein concentrations (%) in milk of otariids (sea lions and fur seals) for which data are available in early lactation.

Species	Lipid	Protein	Source
Sea lions			
Australian (*Neophoca cinerea*)	21.6	—	Gales et al. 1996
South American (*Otaria flavescens*)	38.6 ± 3.1	11.1 ± 1.2	Werner et al. 1996
California (*Zalophus californianus*)	31.7	8.6	Oftedal et al. 1987a
Galapagos (*Z. c. wollebaeki*)	21	09	Trillmich and Lechner 1986
New Zealand (*Phocarctos hookeri*)	21.3 ± 8.1	9.2 ± 2.4	This study
Fur seals			
Antarctic (*Arctocephalus gazella*)	37.9–42.1	6.7–11.0	Arnould and Boyd 1995b
Galapagos (*A. galapagoensis*)	29.4 ± 5.9	09.9 ± 1.4	Trillmich and Lechner 1986
Subantarctic (*A. tropicalis*)	45.0 ± 3.7	13.4 ± 1.4	Georges et al. 2001
Australian (*A. pusillus doriferus*)	30	6.5–16.2	Arnould and Hindell 1999
Cape (*A. pusillus pusillus*)	23.2 ± 8.2	10.8 ± 1.2	Gamel et al. 2005

was not exceptional and unlikely to be due to contamination of the milk samples with salt water.

The duration of period of maternal attendance and duration of maternal foraging trips are important factors determining the lipid content of milk in some pinnipeds (Costa 1991b). However, a significant relationship was not observed between milk lipid concentration, foraging trip duration (duration of maternal foraging trips preceding milk sampling), and duration of period between haul-out to milk sampling in the NZ sea lions (Table 5). This is similar to the observation of Australian sea lions (*Neophoca cinerea*) by Kretzmann et al. (1991). These results suggest that lactating otariid species making short foraging trips have lower milk fat concentrations than those females that make longer foraging trips. Furthermore, examination of data from the present study, although covering only the 1st part of early lactation, indicated that milk lipid and energy content increased with pup age, as reported in several species of otariids (Arnould and Boyd 1995a; Arnould and Hindell 1999; Costa and Gentry 1986; Gales et al. 1996; Georges et al. 2001; Oftedal et al. 1987a; Trillmich and Lechner 1986). In contrast, Kretzmann et al. (1991) failed to find a correlation in Australian sea lions between milk lipid concentration and pup age (stage of lactation). Year had a significant effect on milk protein concentration in NZ sea lions and its concentration fluctuated throughout the study period; this was inconsistent with values reported in other otariids (Fig. 2).

There was a temporal (year and month) variation in milk components that reflects the effect of both individual characteristics and environmental factors on milk composition (Fig. 2). This variation was further supported by the low value of repeatability of the concentration of the components (lipid, protein, and energy) of milk from females captured either twice in any 1 year or in more than 1 year. A high value of repeatability for a milk component indicates that animal factors, both genetic and permanent effects, explain most of the total variation for that component. A low value of repeatability indicates that environmental factors such as variation of food sources associated with year and month explain most of the total variation for that component.

Although it is not possible to partition the variation in these data between individual characteristics and environmental effects, it is appropriate to note that if a lactating female is in poor body condition, fat concentration in the milk may be lower, but protein concentration in milk invariably falls when food intake or dietary protein is reduced (Derrickson and Lowas 2007). Consequently, the lower concentration of protein in milk decreases postnatal growth of the offspring (Derrickson and Lowas 2007). In support of this argument, the years of significantly lower milk lipid and energy content (2001; Fig. 2) and protein content (2002 and 2003; Fig. 2) in milk coincide with the reported lower growth rates of NZ sea lion pups in comparison with other sea lion species, except for Australian sea lions (Chilvers et al. 2006a).

In addition to low pup growth rates, if compared with other sea lion species, both NZ sea lions and Australian sea lions have lower milk quality, make shorter foraging trips, and forage and dive at their physiological limits (Chilvers et al. 2005, 2006b; Costa and Gales 2003). Presumably with NZ sea lions and Australian sea lions, expending more energy on foraging than in other sea lion species results in the production of a lower-energy milk than their counterparts. Therefore, it is possible that under these conditions, NZ sea lions and Australian sea lions are having difficulties in provisioning their pups adequately, which has consequences for their population viability.

Fatty acid analysis carried out on milk and blubber samples from lactating sea lions from the same Auckland Islands population have shown changes in prey composition between years and support the idea of variability of local environmental conditions prior to and after the summer (Meynier et al. 2010; Riet-Sapriza 2007); in addition, there also are suggestions that the presence of squid trawl fisheries around the Auckland Islands may influence the availability and distribution of preferred sea lion prey (Chilvers et al. 2011; Meynier 2008; Robertson and Chilvers 2011). It is also possible that the rate of metabolism (mobilization and deposition) of depot fat during the highly demanding period of lactation changed in response to limited food resources or low quality of prey in the NZ sea lion diet (Meynier et al. 2009). This is supported by the annual variability in maternal body mass observed in summer (Fig. 3b). Thus, it would appear that interannual variations in prey availability due to fisheries competition or natural causes or in rate of metabolism of depot fat, or both, can greatly impact the quality of sea lion milk and, by implication, reproductive success, neonatal survivorship, and recruitment.

Maternal BCI was positively correlated to milk lipid concentration, energy content, and protein concentration in milk, confirming that lactating females with good body condition produced a more energy-rich milk than did leaner nursing females (Table 5). Furthermore, our results showed that BCI improved with age; thus, milk quality increased with age but it was probably more related to the significant effect of BCI rather than to age of the mother. The relationship between lipid and energy content of milk and BCI also has been reported by Georges et al. (2001) in subantarctic fur seals (*Arctocephalus tropicalis*) and by Arnould and Hindell (1999) in lactating Australian fur seals. In concordance with reports for Australian fur seals (Arnould and Hindell 1999), and Antarctic fur seals (*Arctocephalus gazella*—Arnould and Boyd 1995a), maternal body mass in NZ sea lions was significantly correlated with milk lipid, protein concentration, and energy content (Table 5); however, these results are inconsistent with observations in Australian sea lions (Gales et al. 1996; Kretzmann et al. 1991). The significant correlation between maternal body mass and protein concentration in whole milk has not previously been reported in otariids (Table 5). A decrease in protein concentration in the milk is an indication of malnutrition in dairy cows and mice (Derrickson and Lowas 2007; Grainger et al. 1982; Thomson et al. 1997). Thus, it is possible that low milk protein concentration in NZ sea lion

females could be used as a marker for malnutrition or dietary insufficiency.

Examination of our data, in conjunction with parallel studies on foraging (Chilvers 2008; Chilvers and Wilkinson 2009; Chilvers et al. 2005) and diet (Meynier et al. 2009) of NZ sea lions, suggests that the concentrations of both lipid and protein in milk can act as indirect indicators of nutrient intake in lactating sea lions. Given that NZ sea lions are a nationally critical species in decline (Baker et al. 2010; Geschke and Chilvers 2009), the relationship between the temporal (yearly and monthly) variations in milk composition, maternal body mass, and reproductive success and changes in food supply in relation to natural perturbations or fisheries resource competition warrants further investigation to disentangle this relationship and implement appropriate management initiatives.

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