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CHAPTER 6

THE BEHAVIOR, PHYSIOLOGY, AND ANATOMY OF LACTATION IN THE PINNIPEDIA

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1. INTRODUCTION

Lactation represents a major proportion of maternal reproductive effort. In ungulates the energetic costs of lactation comprise 75–80% of the total energetic costs of reproduction (Oftedal, 1985). Although pinnipeds feed at sea, they return to land or ice to give birth and to nurse their young (Fig. 1) (Bonner, 1984). Thus, the bulk of a female's reproductive expenditure is in an environment in which she cannot feed. The temporal separation of feeding and lactation is achieved by a wide range of behavioral, physiological, and anatomic adaptations.

The three pinniped families have adopted different lactation strategies. The phocids (true seals) accumulate energy and nutrient reserves prior to parturition. Lactation is a relatively brief period of 4–50 days characterized by maternal fasting, rapid weight gain by the pup, and abrupt weaning when the mother departs to feed at sea. The otariids (fur seals and sea lions) alternate brief periods of nursing with foraging

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trips at sea. The ability to replenish maternal reserves during lactation permits an extended period of care (typically 4–12 months) during which pups grow slowly. The sole surviving odobenid (the walrus) deviates from the pinniped norm in that the pup accompanies the mother and suckles at sea after leaving the natal site. Concurrent feeding and lactation after departure enables weaning to be gradual and lactation to persist for up to 2 years (Fay, 1982).

Lactation patterns have received much attention in pinnipeds, in part because many species are accessible and easily observed during this period. The predictability of breeding site and time, gregariousness, relative immobility on solid substrate, and site tenacity of most pinniped species facilitate studies in which extended observation, marking of individuals, or repeated captures are required.

In this paper we review data on behavioral, physiological, and



FIGURE 1. Lactating southern elephant seal with her pup on Macquarie Island. Note the unusual circumstance of milk squirting from the lower teat while the pup pauses during suckling. (Photograph courtesy of M. M. Bryden.)

anatomic aspects of lactation in pinnipeds. Although behavior has historically received more attention than other aspects of the lactation process, quantitative measurement of milk production and lactation energetics is an area of much recent activity. Anatomic and secretory adaptations associated with the diverse lactation patterns of pinnipeds are of particular interest; unfortunately, data are limited to a few species. A listing of the common and scientific names of the 33 species of extant pinnipeds is provided in Table I. For the sake of simplicity, species will be referred to by common names in this paper.

2. BEHAVIOR AND ECOLOGY OF LACTATION

2.1. Distribution and Breeding Habitat

Pinnipeds are widespread in distribution, ranging from the Arctic to the Antarctic. Otariids are found predominantly in subtropical to temperate regions, whereas phocids tend to inhabit temperate to polar latitudes (Table I). One otariid, the Antarctic fur seal, ranges into polar regions, and another, the Galapagos fur seal, is the only extant pinniped with a range that is exclusively tropical. The walrus has an Arctic and subarctic distribution. Differences among the three pinniped families in current patterns of distribution and whelping habitat can be traced to paleoecological differences in evolutionary origin and subsequent radiation (Ray, 1976; Repenning, 1976; Repenning et al., 1979).

All otariids whelp and rear young on land, especially on remote islands or regions of mainland inaccessible to humans. Otariids that inhabit areas that may be covered seasonally by pack ice (for example, Steller sea lion, northern fur seal, subantarctic fur seal, Cape fur seal) give birth in late spring or summer when the areas are free of ice. By contrast, phocids use diverse substrates for whelping and rearing of young. In temperate regions phocids may give birth on remote islands, on secluded mainland beaches, or on islands now inhabited by people (Bonner and Witthames, 1974; Scolaro, 1976; LeBoeuf and Panken, 1977; Mansfield and Beck, 1977; Renouf et al., 1981; Alcorn, 1984). In the Arctic, Antarctic, and extreme temperate latitudes, phocids whelp on ice. Ice can be categorized as pack ice (floating ice shelves), which is structurally unstable and variable in distribution, or as fast ice (grounded ice sheets, sometimes referred to as sea ice), which is very stable and is thus more akin to land (Bunt, 1968; Knox, 1970). Ten species are known to whelp on pack ice and three whelp on fast ice (Table I). The walrus gives birth on the pack ice of the Arctic.

TABLE I
Geographic Distribution of Pinnipeds in the Northern (N) and
Southern (S) Hemispheres^a

Taxa	Tropical (0–20°)	Subtropical (20–40°)	Temperate (40–60°)	Polar (60–80°)
Phocidae				
<i>Pack-ice whelping</i>				
Bearded seal, <i>Erignathus barbatus</i>			N	N
Caspian seal, <i>Phoca caspica</i>			N	
Crabeater seal, <i>Lobodon carcinophagus</i>			S	S
Grey seal, <i>Halichoerus grypus</i>			N	N
Harp seal, <i>Phoca groenlandica</i>			N	N
Hooded seal, <i>Cystophora cristata</i>			N	N
Leopard seal, <i>Hydrurga leptonyx</i>			S	S
Ribbon seal, <i>Phoca fasciata</i>			N	N
Ross seal, <i>Ommatophoca rossi</i>				S
Spotted seal, <i>Phoca largha</i>			N	N
<i>Fast-ice whelping</i>				
Baikal seal, <i>Phoca siberica</i>			N	
Ringed seal, <i>Phoca hispida</i>			N	N
Weddell seal, <i>Leptonychotes weddellii</i>			S	S
<i>Land whelping</i>				
Hawaiian monk seal, <i>Monachus</i> <i>schauinslandi</i>		N		
Harbor seal, <i>Phoca vitulina</i>		N	N	
Mediterranean monk seal, <i>Monachus monachus</i>		N		
Northern elephant seal, <i>Mirounga angustirostris</i>		N	N	
Southern elephant seal, <i>Mirounga leonina</i>		S	S	

TABLE I (Continued)

Taxa	Tropical (0–20°)	Subtropical (20–40°)	Temperate (40–60°)	Polar (60–80°)
Otariidae				
Antarctic fur seal, <i>Arctocephalus gazella</i>			S	S
Australian sea lion, <i>Neophoca cinerea</i>		S		
California sea lion, <i>Zalophus californianus</i>	S	N		
Cape fur seal, <i>Arctocephalus pusillus</i>		S	S	
Galapagos fur seal, <i>Arctocephalus galapagoensis</i>	S			
Guadalupe fur seal, <i>Arctocephalus townsendi</i>		N		
Hooker's sea lion, <i>Phoca hookeri</i>			S	
Juan Fernandez fur seal, <i>Arctocephalus philippii</i>		S		
New Zealand fur seal, <i>Arctocephalus forsteri</i>		S	S	
Northern fur seal, <i>Callorhinus ursinus</i>		N	N	
South American fur seal, <i>Arctocephalus australis</i>	S	S		
Southern sea lion, <i>Otaria byronia</i>	S	S	S	
Steller sea lion, <i>Eumetopias jubatus</i>		N	N	
Subantarctic fur seal, <i>Arctocephalus tropicalis</i>		S	S	
Obodenidae				
Walrus, <i>Odobenus rosmarus</i>			N	N

^aData are from FAO (1982) and Harrison and Ridgway (1981). Zones of latitude are taken from Kormondy (1969).

Variation in whelping habitat occurs within species in some phocids. The Weddell seal, normally a fast-ice species, uses beaches on nearby islands in years of bad ice (E. A. Smith and Burton, 1970; Popov and Krylov, 1978). The southern elephant seal whelps on ice rather than on land in years when the ice does not recede from around Signy

TABLE II
Duration of Pupping Season and Lactation Period in Pinnipeds^a

Species	Pupping duration (days)	Lactation duration (days)	Data quality ^b	References
Phocids				
Pack-ice whelping				
Hooded seal	15	4	n = 15	Bowen et al. (1985, 1986a)
Harp seal	10	12	n = 33	Bowen and Sergeant (1983), Kovacs (1986)
Bearded seal	24	12-18	nd	Burns (1981a)
Grey seal	36	17 ^c	n = 38	Boness (1979)
Caspian seal	—	21	nd	Ivashin et al. (1972)
Ribbon seal	—	21-28	nd	Burns (1981b)
Spotted seal	—	35	nd	Golt'sev and Fedoseev (1970)
Crabeater seal	15	14-21	est	Naito and Nishiwaki (1972)
	—	35-42	est	Laws (1958)
Leopard seal	—	28	nd	Siniff et al. (1979)
	—	~30	nd	Tikhomirov (1975)
Fast-ice whelping				
Weddell seal	40	33-44	n = 10	Kaufman et al. (1975)
	—	50	n = 50	Lindsey (1937)
Ringed seal	30	~60	est	McLaren (1958)
Baikal seal	~60	60	nd	Pastukhov (1973a)
Land whelping				
Southern elephant seal	45	23	n = 60	Carrick et al. (1962)
	—	23	n = 28	Condy (1980)
Northern elephant seal	—	24	n = 12	McCann (1982)
Harbor seal (concolor)	36	27	n = 44	Reiter et al. (1978)
	32	33	n = 4	Boulva and McLaren (1979), J. W. Lawson (personal communication)
Harbor seal (richardsii)	—	21-35	nd	Bishop (1967)
	75	35-42	est	Bigg (1969)

Harbor seal (<i>stejnegeri</i>)	—	90	nd	Belkin et al. (1969)
Harbor seal (<i>vitulina</i>)	21	28	nd	Venables and Venables (1955)
Hawaiian monk seal	135	39	n = 16	Alcorn (1984)
Mediterranean monk seal	—	42–49	nd	Boulva (1979)
Otariids				
Antarctic fur seal	30	117	n = 8	Payne (1979), Kerley (1983), Doidge et al. (1986)
Northern fur seal	60	120	est	Peterson (1965)
Steller sea lion	60	120–365 ^d	est	Gentry (1970), Edie (1977), Pitcher and Calkins (1981)
Subantarctic fur seal	45	300–330	est	Best (1981), Kerley (1983), Roux and Hess (1984)
New Zealand fur seal	18	300–365	est	Stirling (1971), Miller (1975)
Cape fur seal	30	300–330	nd	Rand (1955), Stirling (1970)
California sea lion	—	≤ 365 ^d	nd	Stirling and Warneke (1971)
	45	≤ 365 ^d	nd	Peterson and Bartholomew (1967), B. S. Stewart and Yochem (1984)
Australian sea lion	180	~365	nd	Marlow (1975), Ling and Walker (1976)
Southern sea lion	60	≤ 365 ^d	nd	Hamilton (1934)
Hooker's sea lion	30	~365	nd	Marlow (1975)
Galapagos sea lion	60	—	—	Best (1974)
	~180	≤ 365 ^d	nd	Trillmich (1979)
South American fur seal	~90 ^e	365–730	7% of 41 ^f	Trillmich and Majluf (1981), Trillmich et al. (1986)
Galapagos fur seal	—	270–365	nd	Vaz Ferreira (1956)
	~90	~730	nd	Trillmich (1979)
Odobenids				
Walrus	~60	730–1095	est	Fay (1982)

^aData converted to days on the assumption that 1 week equals 7 days, 1 month equals 30 days, and 1 year equals 365 days.

^bData refer to lactation duration; est, indirect estimate; nd, no data; n, number of individuals followed to weaning.

^cData are from a land-breeding colony of grey seals.

^dYearlings have been observed suckling, but the percentage doing this is unknown if the quality of data is shown as nd.

^eRecent unpublished observations by P. Majluf reveal that this value should be about 45–60 days.

^fOut of 41 females at a rookery, 7% were still nursing yearlings as well.

Island prior to the onset of parturition (Laws, 1956). The grey seal is the only species with some colonies that produce pups on land (Davies, 1949; Hewer, 1974; Anderson et al., 1975; Boness and James, 1979) and others that typically give birth on pack ice (Curry-Lindahl, 1975; Hook and Johnels, 1972). It has been suggested that the grey seal originated as a pack-ice species and has secondarily taken up land-whelping (McLaren, 1960; Boness, 1979).

Migratory behavior of pinnipeds may be related to whelping habitat. Most pack-ice phocids migrate at the end of the pupping season, whereas fast-ice and terrestrial phocids appear to be nonmigratory. The migration of pack-ice species may reflect a lack of adequate food supplies in the vicinity of the ice at the end of lactation (Bowen et al., 1985). Although nonmigratory, the fast-ice and terrestrial phocids radiate for distances of several hundred km to more than 1000 km from the whelping grounds to feed after lactation (Hewer, 1974; Condit and LeBoeuf, 1984).

Otariid females are nonmigratory, with the exception of northern fur seal females (Lander, 1979), which migrate south after the relatively short lactation period (Table II). In the Steller and California sea lions, males migrate north after mating with females on the rookeries (Mate and Gentry, 1979; Bigg, 1973). Otariid males are not constrained to forage near the rookery, since they play no role in caring for the young.

The walrus gives birth on pack ice, but in contrast to phocids, appears to use the floating ice as a means of conveyance to new foraging areas for benthic invertebrates on the outer banks of the Bering Sea (Fay, 1982). Like the phocids of the pack ice, the walrus is migratory. In the spring, as temperatures rise and the ice breaks up, animals move northward, where new ice is beginning to form (Fay, 1982).

2.2. Timing of Whelping

All pinnipeds for which information is available give birth seasonally. Both sexes aggregate when pupping begins, and mating occurs a few days to a few weeks postpartum. For terrestrial and fast-ice species, the sites where seals aggregate are very precise from year to year because of the long-term stability of these substrates (for example, McLaren, 1958; Hewer, 1960; Peterson, 1965; Gentry, 1970; T. G. Smith, 1973; LeBoeuf, 1974; Kaufman et al., 1975; Boness, 1979; Campagna, 1985). For pack-ice species, the location of whelping aggregations is less precise, but normally occurs in the same region from year to year (Lavigne, 1976; Burns and Frost, 1979).

The duration of the pupping season varies across species, ranging

from about 10 to approximately 180 days and is related to whelping habitat (Table II). Pack-ice phocids tend to have the shortest pupping seasons, 10–36 days. Fast-ice and terrestrial phocids and most otariids produce pups over a period of about 30–60 days. The periods of pupping of two otariids (Galapagos sea lion and Australian sea lion) and one phocid (Hawaiian monk seal) are markedly longer than those of other species in their respective families (Table II). All three species occur at latitudes that are among the lowest of their respective families, but not all low-latitude species have extended pupping seasons. Ling and Walker (1976) postulate that the long season in the Australian sea lion results from a lack of the constraint that is placed on other species by extremely harsh seasonal conditions. Consistent with this, Gentry et al. (1986) argue that short pupping periods in the Antarctic and northern fur seals are related to seasonal changes in climate and food supply. However, if seasonality alone was the major factor controlling variation in the length of pupping periods, we would expect more temperate and subtropical species to have longer periods.

Other factors of possible importance include the instability of pack ice and ability of males to remain at the breeding grounds. Pack ice can break up and shift several kilometers overnight (Hook and Johnels, 1972) and the likelihood of this increases as spring approaches. These conditions should result in an increased synchronization of pupping. Anderson and Fedak (1985) present data suggesting that the energetic demands of fasting and conflict between males force some grey seal males to depart from the rookery before all females are inseminated. Females that pup outside the primary period of male aggregation may be at a selective disadvantage in that prime males may have already departed to replenish their body stores.

2.3. Maternal Behavior and Suckling Patterns

2.3.1. Perinatal Behavior

Pinniped females haul out at parturition sites shortly before giving birth. For example, harp seals typically come onto the ice the day they give birth, whereas Steller sea lions haul out an average of 4 days prior to birth (Sandegren, 1970; R. E. A. Stewart et al., 1981).

A bond between the mother and neonate is formed immediately after parturition through frequent nosing and vocalizations, which provide an opportunity for recognition of individual odors and vocal traits. Among phocids, the interactions typically take the form of the female sniffing the pup, although pups may vocalize (Fogden, 1971; LeBoeuf

et al., 1972; Burton et al., 1975). Among otariids, females vocalize to their pups with special "pup attraction" calls and nose them frequently and pups respond to their mothers' calls (Bartholomew, 1959; Sandegren, 1970; McNab and Crawley, 1975; Trillmich, 1981). The combined auditory and olfactory exchanges between otariid females and pups are associated with few errors in recognition during subsequent suckling events. Individual recognition is important for otariids because females leave the rookery for several days at a time and upon return must relocate their pups among many others. By contrast, although phocid females tend to stay in close proximity to their pups throughout lactation, nursing of foster and unrelated pups by females is much more common among phocids (Fogden, 1971; Stirling, 1975; Alcorn, 1984). This may be associated with overcrowding or other factors that cause females to move into the water between periods of nursing (for example, Fogden, 1971).

Females of all species are protective of their pups, particularly just after parturition. Threats involving visual and vocal components are used by females against conspecifics of either sex that approach too closely (for example, Boness et al., 1982). In the northern elephant seal, there is lower mortality among pups whose mothers are relatively aggressive compared to pups of less aggressive mothers (Christenson and LeBoeuf, 1978). On the whole, otariid and odobenid females seem to be more tolerant of conspecifics near their pups than phocids, but this has not been addressed quantitatively in many species.

2.3.2. Problems in Quantifying Suckling

Not all quantitative studies of suckling in free-ranging pinnipeds can be compared directly, because definitions and exactness in measurements have differed among studies. Pinniped pups do not remain attached to the teat until completion of the suckling session, unlike the young of some mammalian species (Drewett, 1983; Hall, 1983). A pup usually sucks on a teat for a short period, breaks contact, and then returns either to the same or a different teat. Detailed examination of suckling sessions in three species indicates variability in the pattern of periods on and off teats. Grey seals in the Orkney Islands exhibit a pattern of sucking for about 6 min with very few breaks or shifts from one teat to another, followed by a secondary period of up to 15–20 min in which there are frequent teat changes (Fogden, 1971). Weddell seal sessions involve either frequent teat changes or relatively unbroken sucking rather than a combination of both within a single session (Tedman and Bryden, 1979). Suckling sessions in captive Cape fur seals are

more uniform, with on-teat durations of about 24 sec and off-teat intervals averaging 36 sec (Carnio, 1982).

Suckling durations reported in the literature may refer only to on-teat duration or may include both on-teat and off-teat intervals (Table III). In some cases, insufficient detail is given to determine how duration has been defined. These methodological differences can result in spurious differences when comparing species. For example, on-teat time comprises 68, 45, and 40% of total session duration (including off-teat intervals) in northern elephant seals (LeBoeuf et al., 1972), Cape fur seals (Carnio, 1982), and California sea lions (D. J. Boness, K. A. Ono, and O. T. Oftedal, unpublished), respectively.

Cumulative on-teat duration would seem the most useful measure of suckling if the intent is to correlate suckling behavior to milk ingestion. Although there is no certainty that any particular sucking action results in milk flow, inclusion of off-teat intervals in measuring suckling duration only adds an additional source of variation. For present purposes a "suckling session" consists of both on-teat periods and short breaks between them. A long break or transition to other activity terminates a session. Conventions adopted in studies of suckling behavior should be well defined such that meaningful interpretation of results is possible.

2.3.3. Suckling Behavior

Suckling may be initiated by the mother or the pup. Weddell, northern elephant, and harbor seal pups usually initiate suckling by approaching, vocalizing to, and nuzzling the female (LeBoeuf et al., 1972; Tedman and Bryden, 1979; Renouf and Diemand, 1984). In the northern fur seal, the pup initiates suckling about 60% of the time and most of the other suckles are begun through a mutual process; females rarely are solely responsible for initiating suckles (Macy, 1982). Sandegren (1970) reports that Steller sea lion females initiate suckling in the first few days following birth, but does not indicate whether this behavior changes with pup age.

A few studies have examined whether the female or the pup terminates suckling sessions. It is usually reported that pups terminate sessions (Fogden, 1971; Macy, 1982; Carnio, 1982). Harbor seal females initially terminate about half of the sessions and the proportion increases as pups get older (Renouf and Diemand, 1984).

Temporal parameters of suckling have been measured in several phocids and otariids (Table III). Data representing cumulative on-teat time within suckling sessions are available for three of the phocids and

TABLE III
Temporal Parameters of Suckling in Pinnipeds

Species	Suckling duration (min)	Session frequency (h ⁻¹)	Intersession interval (h)	Daily duration ^e (h/24 h)	Pup age-related changes ^d			References
					Duration	Frequency	Daily duration	
Weddell seal	30.0 ^c	0.34	2.9	4.1	—	—	—	Tedman and Bryden (1979)
Grey seal	10.4 ^b	0.33	3.0	1.4	+	0	+	D. J. Boness (unpublished)
Harp seal	7.3 ^b	0.40	2.5	1.2	+	—	0	R. E. A. Stewart (1983)
Northern elephant seal	6.8 ^b	0.31	3.2	0.9	+	+	+	LeBoeuf et al. (1972)
Southern elephant seal	5.8 ^c	0.56	1.8	1.3	+	+	+	Bryden (1968)
Subantarctic fur seal	21.5 ^b	0.83	1.2	7.2	nd	nd	nd	Bester (1977)
Guadalupe fur seal	18.5 ^c	0.20	~5.0	1.5	nd	nd	nd	Pierson (1978)
Steller sea lion	16.2 ^b	0.37	2.7	2.4	+	—	—	Sandegren (1970), Higgins (1984)
California sea lion	10.7 ^b	0.41	2.4	1.8	nd	nd	nd	D. J. Boness (unpublished)
Northern fur seal	8.5 ^c	—	—	—	nd	nd	nd	Macy (1982)

^aSuckling duration includes off-test intervals.

^bSuckling duration is cumulative on-test time.

^cNot enough information is given in the study to discern what the duration includes.

^d+, Increase; —, decrease; 0, no change; nd, no data available.

^eData are expressed relative to time mother is present.

^fThese changes in suckling parameters cover only the first one-tenth of the lactation period.

three of the otariids in Table III. Among these species, the average duration of suckling sessions in otariids is about twice as long as that of phocids (mean \pm standard deviation of 16.1 ± 5.40 as compared to 8.2 ± 1.95 min). The otariids also suckle more frequently (when the mother is present at the rookery) than do the phocids, but the difference is of smaller magnitude than the difference in duration (0.53 ± 0.25 as compared to 0.35 ± 0.10 suckle/h). These patterns of frequency and duration of suckling sessions yield calculated mean daily suckling durations of 3.8 h per 24 h ($SD = 2.95$) for the otariids and 1.2 h per 24 h ($SD = 0.25$) for the phocids. The small number of species and differences in variances preclude statistical analysis of these data. The variance in all measures is substantially greater in the otariids than in the phocids. This is predominantly due to the greater average duration and frequency of suckling in the subantarctic fur seal than in the other two otariids. The long daily duration of suckling in the Weddell seal compared to other phocids may simply reflect relatively frequent or long off-teat intervals, since this estimate includes these intervals.

Changes in suckling pattern over the course of lactation differ among species. Daily suckling duration increases with pup age in the grey seal and both elephant seals, decreases with pup age in the Weddell seal, and remains relatively unchanged in the harp seal (Fig. 2). The increasing trend in northern and southern elephant seals is the result of an increase in both session duration and frequency (Bryden, 1968; LeBoeuf et al., 1972). In the grey seal, session duration increases, while frequencies remain the same (D. J. Boness, unpublished). The decrease in daily suckling duration with age in the Weddell seal results from a decrease in both session frequency and duration (Tedman and Bryden, 1979). In harp seals a slight increase in session duration is counteracted by a decrease in session frequency such that daily duration is unchanged (R. E. A. Stewart, 1983).

Changes in suckling behavior over the entire course of lactation have not been published for any otariid, although South American fur seal pups suckle for no more than 1 h per session when they are less than 3 months old, but as yearlings, before they are weaned, suckling durations may exceed two hours (P. Majluf, personal communication). In the Steller sea lion an increase in session duration over the first month after birth is more than compensated by a decrease in frequency such that daily suckling duration decreases (Sandegren, 1970; Higgins, 1984). Nothing is known of subsequent patterns, however. In the absence of longitudinal studies of the behavior of the walrus, little is known about its maternal behavior or suckling patterns. Suckling sessions appear to be intermediate in duration to those of phocids and

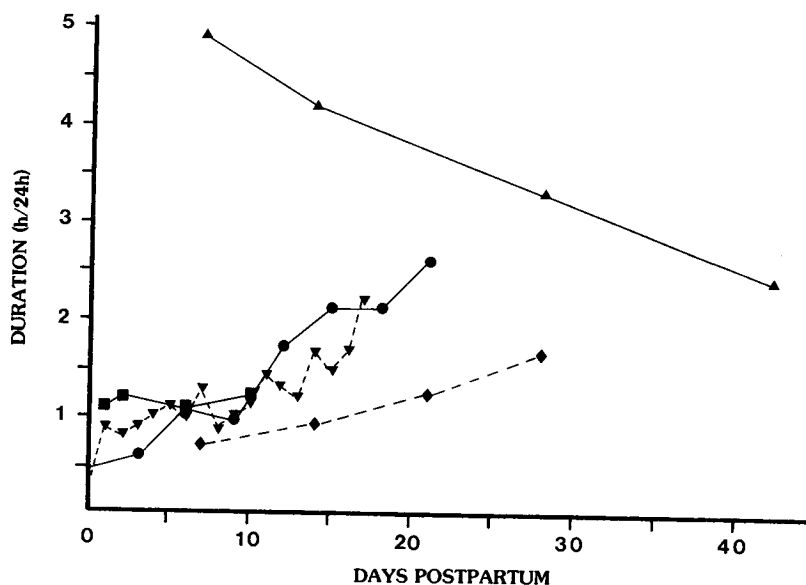


FIGURE 2. The relationship of mean daily suckling duration to pup age in phocids. (▲) Weddell seal, (●) southern elephant seal, (◆) northern elephant seal, (▼) grey seal, (■) harp seal.

otariids, but aquatic suckles are shorter on average than terrestrial ones (11.7 as compared to 16.0 min) (Miller and Boness, 1983; Salter, 1978). There are no data on the frequency of suckling.

2.3.4. Patterns of Maternal Attendance

Phocid females remain in the vicinity of the pupping site throughout lactation. Females of some species stay in close proximity to their pups, whereas females of others leave their pups and go into the water, but apparently remain nearby (Table IV). Most pack-ice species enter the water during the lactation period, although the hooded seal remains with its pup on the ice. This may relate to the extremely short lactation period observed in this species (see Section 2.4). Among those species in which females spend time in the water, as much as 70% of their time may be spent there, as is the case in harp seals (R. E. A. Stewart, 1983). In four of these species, pups follow their mothers, although this usually does not occur immediately after birth. The grey seal exhibits both types of attendance patterns when pupping on land, but not enough

information is available to know if this is true of ice-pupping populations as well.

One obvious reason for females to spend time in the water is to feed on prey available in the immediate vicinity. Stomach samples taken from females at pupping sites contained food in about half the species in which females enter the water during lactation (Table IV). The amount consumed by lactating females is markedly reduced in comparison to the amount ingested outside the lactation period, however. The lack of evidence of feeding in some species in which females spend time in water could reflect insufficient data or may indicate that water entry may be related to factors other than food. Among factors that might be important are avoidance of thermal stress (Pierotti and Pierotti, 1980; R. E. A. Stewart, 1983), avoidance of either land- or ice-based predators (Table IV), and mating activities (Stirling, 1983). Animal movements may also be influenced by population density at pupping sites.

Otariid females attend their young continuously for a short period after birth, but then alternate between periods of foraging at sea and nursing on land ("feeding cycles"). Intraspecific variation is apparent in feeding cycles in at least three species in Table V. Part of this variation might be attributed to varying levels of accuracy of the data, but differences also relate to pupping sites and year of study. For example, northern fur seal females at St. Paul Island stayed at sea longer than females at St. George Island (Gentry and Holt, 1986). St. Paul is further from the continental shelf where fur seals feed than is St. George. Likewise, California sea lion females at San Nicolas Island had longer foraging trips in 1983 and 1984, during a food shortage caused by El Niño, compared to 1982 and 1985 (mean \pm SD: 1982, 1.4 ± 0.32 ; 1983, 2.0 ± 0.78 ; 1984, 2.5 ± 0.72 ; 1985, 1.7 ± 0.54 ; Scheffe's range test indicated 1982 and 1985 $<$ 1984, $P < 0.01$) (K. A., Ono, D. J. Boness, and O. T. Oftedal, unpublished).

Substantial interspecific variation occurs in duration of foraging periods (1–10 days; Table V), whereas there is less variation in the length of time to first departure (4–10 days) and the duration of periods of presence at the rookery (0.5–3 days). The variation in duration of foraging periods might reflect differences in type and accessibility of food. The species with the longest foraging periods, the northern fur seal, is a pelagic feeder, traveling as much as 250 km to feed (Scheffer, 1970; Lander and Kajimura, 1982; Stirling, 1983). Similarly, Antarctic fur seal females forage at sea for over 4 days on average and are known to travel approximately 200 km to feed (Croxall et al., 1985). In contrast, California sea lion and Cape fur seal females are absent on average for only 2.5 and 2.9 days, respectively, while feeding in shallow water less

TABLE IV
Aquatic Behavior and the Occurrence of Predators at Phocid Pupping Sites

Species	Time spent in water by females	Do pups accompany females in water?	Evidence of feeding by females	Predators at pupping site	References
			Pack-ice		
Bearded seal	Some	Yes	None ^a	Infrequent, polar bears	Burns (1970, 1981a)
Caspian seal	Large proportion	No	None	Wolves, large eagles	Ivashin et al. (1972), Popov (1979)
Grey seal	≤49% ^b	No ^b	None	Sharks	Brodie and Beck (1983), Coulson and Hickling (1964), Fogden (1971), D. J. Boness (unpublished), Anderson and Harwood (1985)
Harp seal	≤70%	No	Yes	Polar bears	Sivertsen (1941), R. E. A. Stewart (1983), R. E. A. Stewart and Murie (1986)
Hooded seal	None	No	None	Polar bears	Shepeleva (1971), Bowen et al. (1985)
Ribbon seal	Large proportion	No	None	None	Burns (1981b), Frost and Lowery (1980)

Spotted seal	Some	No	Yes	Polar bears, wolves	Burns et al. (1972), Bonner (1979a)
			<i>Fast-ice</i>		
Baikal seal	Some	No	Yes	Infrequent, brown bears	Pastukhov (1975b), Thomas et al. (1982)
Ringed seal	Some	Yes	Yes ^a	Frequent, polar bears	McLaren (1958), Stirling and McEwan (1975), Smith and Hammil (1981)
Weddell seal	≤56%	Yes	None	None	Kaufman et al. (1975), Demaster (1979)
			<i>Terrestrial</i>		
Harbor seal	Large proportion	Yes	Yes	Infrequent, eagles, sharks	Bonner (1979b), Boulva and McLaren (1979), Renouf (1984)
Hawaiian monk seal	Some	Yes	None	Sharks	Kenyon and Rice (1959), Alcorn (1984)
Northern elephant seal	None	No	None	None	LeBoeuf et al. (1972)
Southern elephant seal	None	No	None	None	Laws (1956), McCann (1982)

^aEvidence indicates that pups may begin feeding on solid food before being weaned.

^bIn some colonies females do not go into the water nor do the pups.

TABLE V
Temporal Parameters of Feeding Cycles in Otariids^a

Species	Time to first departure (days)	Absence duration (days)	Presence duration (days)	Percent time absent	Reference
Cape fur seal	4.3	2.9	2.4	54.4	David and Rand (1986)
Antarctic fur seal	6.9	4.3	2.1	64.9	Doidge et al. (1986)
Northern fur seal	8.0	9.4	2.0	—	Peterson (1968)
	~4-7	7.7	1.5	—	Bartholomew and Hoel (1953)
Galapagos fur seal	7.4	5.9	2.2	73.0	Gentry and Holt (1986)
California sea lion	7.3	1.3 ^b	1.0 ^b	55.3	Trillmich (1986a)
	7.9	2.5	1.4	52.3	D. J. Boness (unpublished)
	6.8	0.8	0.5	52.0	Trillmich (1986b)
Steller sea lion	9.0	0.7	0.7	—	Sandegren (1970)
	6.7 ^c	~2 ^c	~1 ^c	50.0 ^c	Higgins (1984)
Guadalupe fur seal	8.8	—	—	—	Pierson (1978)
New Zealand fur seal	~7	5.0	1.2	—	Stirling (1970)
	8.5	~1-2	—	—	McNab and Crawley (1975)
	10.0	~3-5	~2-4	—	Miller (1971)
South American fur seal	—	4.6 ^c	1.3 ^c	76.5 ^c	Trillmich et al. (1986)

^aValues are means unless otherwise stated and may reflect observations from more than one rookery or over more than one season.
^bValues are medians; females with 1- to 2-year-old young have slightly different values for absence (0.9 day) and presence (0.5 day).
^cValues obtained in an El Niño year and therefore may not reflect normal years.

than 100 km from the rookery (Fiscus and Baines, 1966; Costa et al., 1985; David and Rand, 1986). Steller sea lions and Galapagos fur seals, known to feed in close proximity to the rookeries, spend only about 1 day on foraging trips (Fiscus and Baines, 1966; Trillmich, 1986).

Feeding cycles change over the course of lactation, but not in a consistent pattern for all species. Maternal foraging trips increase in duration as pups get older in the Cape fur seal, Steller sea lion, and South American fur seal (David and Rand, 1986; Gentry and Holt, 1986; Higgins, 1984; P. Majluf, personal communication) and in one study of northern fur seals (Bartholomew and Hoel, 1953). However, the relationship between age and trip duration is more complex in the California sea lion and a second study of the northern fur seal. Trip duration in California sea lions decreases during the third month postpartum following an increase during the first 2 months. There is a subsequent increase in the length of foraging trips from the fourth to the sixth month postpartum (Boness et al., 1985a). Peterson (1965) found that northern fur seals initially increase the duration of trips to sea, but then decrease the length of time away as their pups get older. It is not clear why the two studies of northern fur seals yield different results. Changes in the duration of foraging trips as pups get older may indicate that the nutritional demands of lactation increase as pups get older (see Section 5.1) and/or that changes occur in prey abundance or composition. Longitudinal data on the duration of periods of presence indicate relatively little variation, although both Cape fur seal and California sea lion females show an initial decrease in duration, after which the duration becomes constant (Peterson, 1965; Boness et al., 1985a; David and Rand, 1986; Gentry and Holt, 1986).

The period of fasting and lactation prior to first departure entails a progressive depletion of female reserves. Interspecific comparisons indicate that neither absolute nor relative female size correlates with length of time to first departure ($r = 0.190$, $n = 9$, $P > 0.05$ and $r = -0.117$, $n = 9$, $P > 0.05$, respectively). However, in the South American fur seal, the length of time a female remains in attendance of her pup is significantly correlated with maternal weight (P. Majluf, personal communication). In the California sea lion, the duration of this period may correlate with the magnitude of female reserves, as evidenced by a significantly shorter initial period of attendance during a severe El Niño that affected food supply (Ono et al., 1985).

In comparison to phocids, otariids have been shown to exhibit a higher frequency and longer duration of suckling during periods of maternal presence. Apparently otariid pups must compensate for periods of maternal absence by increased suckling when mothers are

available. We predict that those otariids with relatively long maternal foraging periods (for example, northern fur seal, Antarctic fur seal) will have relatively long daily suckling durations. Available data do not permit this hypothesis to be tested.

2.4. Duration of Lactation

Lactation duration also varies markedly among and within pinniped families. The phocids typically have short lactation periods, whereas otariids have relatively long lactation periods (Table II). Walruses, which take their pups with them and nurse aquatically, have the longest lactation period of any pinniped (Mansfield, 1958; Loughrey, 1959; Miller and Boness, 1983; Fay, 1982).

The quality of data available on the duration of lactation is quite variable. Known individuals have been followed from parturition to weaning in only a few phocids and one otariid. Many studies have estimated lactation length from census data, and others provide only a qualitative statement without further explanation. The problem is clearly greater in otariids than in phocids, and reflects the difficulty of following individuals over an extended period. In many otariids, lactation length is described as about 1 year because some yearlings are observed suckling (Table II). Few studies, however, have attempted to determine the proportion of the yearling cohort that is still suckling at a given age (Trillmich and Majluf, 1981; Boness et al., 1985b). Construction of weaning curves (for example, Bowen et al., 1985) would permit more meaningful interpretation of the duration of lactation in otariids.

Despite the need for better quantitative data on the duration of lactation, it is obvious that there is substantial variation within each family. Among phocids, the range in duration of lactation is at least in part associated with the stability and harshness of the breeding habitat ($P < 0.05$; Scheffe's range test). Fast-ice species have significantly longer periods of lactation (55.6 ± 7.51 d, $n = 3$) than either pack-ice species (20.3 ± 9.98 d, $n = 9$) or land-whelping species (30.5 ± 7.0 d, $n = 4$). One pack-ice species, the hooded seal, has the shortest lactation period (4 days) known for any mammal (Bowen et al., 1985). Instability of ice due to storms during the lactation period and the potential for polar bear predation may contribute to the selective advantage of a shortened lactation period.

The finding that fast-ice species have longer periods of care than terrestrial species may seem surprising, particularly because ambient conditions on fast ice are typically harsher than on land and, in the

northern hemisphere, polar bears are a known predator on the fast ice. The two northern fast-ice species (ringed seal and Baikal seal) build birth lairs under ice hummocks or snow; the southern species (Weddell seal) does not. These dens can serve both to hide the female and her young from predators and to provide protection against severe surface weather (McLaren, 1958; Pastukhov, 1975b; T. G. Smith and Stirling, 1978). Thus, there could be some advantage to remaining in lairs as long as possible. The relatively long lactation period of the Weddell seal in the southern hemisphere might relate to aquatic predation. The leopard seal preys upon pups that have left the ice (Demaster, 1979).

It has been suggested that variation in lactation duration among fur seals may be related to differences in environmental predictability and climatic harshness associated with latitude. According to Gentry et al. (1986), high latitudes have strong seasonality with severe weather, but conditions are relatively similar from year to year, whereas low latitudes show less seasonal change but are more prone to unpredictable environmental oscillations such as El Niño. They hypothesize that high-latitude conditions favor short lactation periods, whereas low-latitude conditions favor longer periods. The significant negative correlation between duration of lactation and latitude among otariids ($r = -0.73$, $n = 13$, $P < 0.01$) is consistent with this hypothesis (Fig. 3).

The comparison of lactation duration to latitude is confounded with accessibility of food resources, however. The two subpolar species that have the shortest lactation periods, the Antarctic fur seal and the northern fur seal, also feed furthest from the rookery, whereas the Galapagos fur seal feeds in close proximity (see Section 2.3.4). The energetic costs to females associated with returning to the rookery to nurse young will be higher in the two subpolar species and may place a premium on reduction in lactation length. The converse may apply to the Galapagos fur seal. There is no evident relationship between lactation duration and latitude among the nine remaining species in Fig. 3 despite a distributional range from 10° to 50° from the equator. Intraspecific studies of species whose whelping distributions cover a large range (for example, Steller sea lion, southern sea lion, California sea lion, South American fur seal) could help refine our understanding of the relationship of lactation duration to latitude in otariids.

2.5. The Process of Weaning

Weaning tends to be abrupt in phocids. Phocid females simply depart from the rookery at the end of lactation, either just after or just before copulation, and do not return to their offspring (Bryden, 1968;

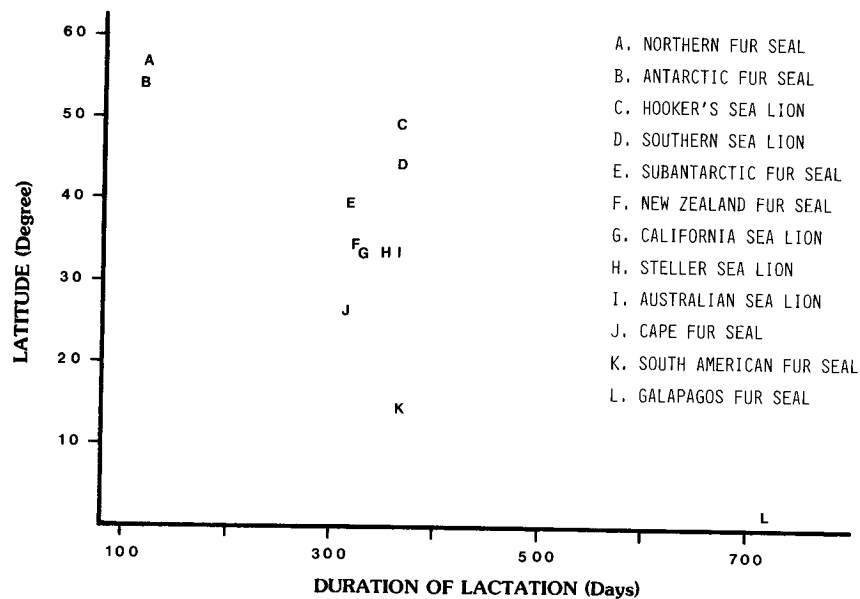


FIGURE 3. The relationship between duration of lactation and latitudinal distribution of otariids. Data are from studies referred to in Table II.

Golt'sev, 1971; Reiter et al., 1978; Boness and James, 1979; Condry, 1979; R. E. A. Stewart, 1983; Bowen et al., 1985). In some species weaned pups remain on the rookery and fast for several days or weeks, but in others the pups depart almost immediately after weaning (Coulson and Hickling, 1964; Bryden, 1968; Ortiz et al., 1978; Condry, 1980; Worthy and Lavigne, 1983a). A more gradual weaning may occur in those phocids in which pups spend time in the water with females (Table IV). Evidence of both milk and solid foods has been found in the stomachs of a few bearded and ringed seal pups (McLaren, 1958; Burns, 1970).

A gradual weaning process probably occurs in most otariids, although considerably more information is needed to confirm this hypothesis. Pups of some species are known to consume both milk and solid food (Hamilton, 1934; Rand, 1959; Trillmich, 1979). In other otariids, pups swim off the rookery during periods when their mothers are absent, but stomach contents have not been examined to determine if feeding occurs. Some evidence of abrupt weaning has been obtained for northern fur seals: 77% of observed pups departed from the rookery before their mothers (Macy, 1982), and females and pups are never sighted together at sea (Gentry and Holt, 1986).

A dichotomy in patterns of behavior emerges from studies of phocids and otariids. The phocids have relatively short lactation periods associated with continuous attendance of pups and fasting by females, whereas the otariids have relatively long periods of lactation, with females alternating between feeding trips at sea and attending their pups at the rookery. Both patterns are different from maternal behavior in most mammals. The accompanying daily suckling durations are not substantially higher than those of terrestrial mammals (Berger, 1979; Reinhardt and Reinhardt, 1981; Whitworth, 1984) despite short lactation periods (phocids) and intermittent suckling (otariids). The explanation of this paradox may be found in the ability of pinnipeds to secrete concentrated milks that permit rapid transfer of energy to the young.

3. THE COMPOSITION OF PINNIPED MILKS

3.1. Factors Affecting Gross Composition

3.1.1. Milk Sampling Procedures

Milk samples have been collected and analyzed for 16 of the 33 extant species of pinnipeds (Table VI). Relative to other mammalian orders this represents a high proportion of species (48%) (Oftedal, 1984a). The data available for pinnipeds vary in quality, however. Many reports are based on only one or a few milk samples obtained opportunistically. Milk has been collected by various sampling methods and at different lactation stages (Table VI). Prior to review of interspecies trends, the possible effects of these variables need to be examined.

The first analysis of a pinniped milk was based on gastric contents of a suckling California sea lion pup (Schroeder and Wegeforth, 1935). More recently, compositional data have been reported for gastric samples from five otariids, four phocids, and the walrus (Table VI). Gastric sampling is an attractive procedure due to the ease of capture and intubation of pups, with minimal disturbance to breeding groups. Unfortunately, gastric samples are apt to be contaminated by salivary and gastric secretions, and are subject to proteolytic and lipolytic enzymes. Milk constituents pass from the stomach at different rates as a consequence of milk curd formation and erosion (Hill et al., 1970). Thus, gastric samples may differ in composition from milk collected directly from mammary glands (Oftedal, 1984a).

In pinnipeds, gastric milk samples are consistently lower in dry matter, fat, and perhaps protein than are mammary samples at the same lactation stage (Table VII). In harp seals, samples obtained by intubation

TABLE VI
Sampling and Analytical Methods Applied in Studies of Milk Composition
in Pinnipeds

Species	Sample type ^a	n	Lactation stage ^b	Analysis type ^c	References
Phocidae					
Bearded seal	G	1	L(14-21)	P	Fay (1982)
Grey seal	M?	1	?	P	Amoroso et al. (1951)
	M?	1	?	F	Meara (1952)
	G	1	L(14)	P,A	Bock et al. (1968)
	X?	1	?	F	Ackman and Burgher (1963)
Harbor seal	?	?	?	(P)	Harrison (1960)
Harp seal	X	2	?	P,M	Sivertsen (1941)
	X?	?	?	(P),F	Jangaard and Ke (1968)
	M+	3	M?(<7)	P,M,F	Cook and Baker (1969)
	?	1	?	P	Jenness and Sloan (1970)
	M+	5	E-L(2-16)	P,M,F	Van Horn and Baker (1971)
	G	26	E-L(0-9)	P	Lavigne et al. (1982)
	G	22	E-L(0-9)	P	R. E. A. Stewart et al. (1983)
	X,M+,G	36	E-L(0-11)	P	O. T. Oftedal, D. J. Boness, and W. D. Bowan, (unpublished)
Hooded seal	X	1	?	P,M	Sivertsen (1941)
	X,G	16	?	P	Shergin et al. (1969)
	X?	?	?	F	Jangaard and Ke (1968)
	X,M+,G	22	E-L(0-4)	P	O. T. Oftedal, D. J. Boness, and W. D. Bowen, (unpublished)
Northern elephant seal	?	7	?	P	Jenness and Sloan (1970)
	M+	9	L(21-28)	P,(M)	LeBoeuf and Ortiz (1977)
	M	48	E-L(0-30)	P,(M),F	Riedman and Ortiz (1979)

TABLE VI (Continued)

Species	Sample type ^a	n	Lactation stage ^b	Analysis type ^c	References
Southern elephant seal	M +	7	E-L(0-21)	P	Bryden (1968)
	M	?	?	—	Shaughnessy (1974)
	M	12	E-L(0-26)	(P,M)	Peaker and Goode (1978) ^d
Weddell seal	M	7	E-M(1-18)	(P),F	Stull et al. (1967)
	M	39	E-L(0-35)	(P)	Kooyman and Drabek (1968)
	?	8	?	P	Jenness and Sloan (1970)
	M +	11	E-L(0-45)	P,(M),F	Tedman (1980)
Otariidae					
Antarctic fur seal	G	1	?	P	Bonner (1968)
California sea lion	G	1	?	P	Schroeder and Wegeforth (1935)
	X	3	E-L(<30-240)	P	Pilson and Kelly (1962)
	M +	28	E-M(0-160)	P	Oftedal et al. (1983)
	G,M +	10	E(2-60)	(P,M)	Trillmich and Lechner (1986)
	M + ,G	64	E-M(0-160)	P,M,F	O. T. Oftedal, D. J. Boness, S. J. Iverson, M. E. Allen, and D. L. Wood (unpublished)
Cape fur seal	X	1	?	(P)	Rand (1955)
	X	1	E(<30)	P	Kerry and Messer (1968)
Galapagos fur seal	M + ,G	27	E(1-30),L(360)	(P,M)	Trillmich and Lechner (1986)
Northern fur seal	M +	5	E-L(0-120)	P,(M),F	Ashworth et al. (1966)
	M	5	E(0->10)	P	Fay (1982; personal communication)
	X	?	M(30-60)	P,M,F,A	Dosako et al. (1983)
	M +	58	E-M(0-60)	(P)	Costa and Gentry (1986)

(Continued)

TABLE VI (Continued)

Species	Sample type ^a	n	Lactation stage ^b	Analysis type ^c	References
South American fur seal	X,G	13	E–L(0–330)	P	Ponce de Leon (1984)
Steller sea lion	?	2	?	P,(M)	Poulter et al. (1965)
Walrus	X,G	4	Odobenidae E(0–30)	P	Fay (1982)

^aSamples were collected from gastric contents of pups (G), by manual expression from live animals with (M+) or without (M) oxytocin, or immediately postmortem by expression or incision (X).
^bStage of lactation characterized as early (E), mid (M), or late (L); range of days after birth indicated inside parentheses.
^cAnalyses reported in source are characterized as proximate analysis (P), mineral analysis (M), fatty acid analysis (F), and amino acid analysis (A); incomplete analysis indicated by parentheses around letter designation.
^dSpecies incorrectly identified as Antarctic fur seal (see Bonner, 1984; M. Peaker, personal communication).

of pups are 9.8 ± 2.21 SE percentage points lower in dry matter and 10.2 ± 1.66 SE percentage points lower in fat than milk samples collected from the mothers of these pups ($n = 8$) (O. T. Oftedal, D. J. Boness, and W. D. Bowen, unpublished observations). The data in Table VII indicate that gastric samples contain about 74, 78, and 83% of the calculated energy content of mammary milk in California sea lions, harp seals, and Galapagos fur seals, respectively. Mean levels of dry matter and fat in gastric samples tend to parallel changes in mammary milk composition over lactation (Table VII) such that gastric samples may reveal relative trends in milk composition even if the absolute values are in error. Thus, Lavigne et al. (1982) were able to demonstrate an age-related increase in fat content of harp seal milk on the basis of gastric samples.

Mammary milk samples have been collected by manual expression from live animals after physical or chemical restraint, or by expression or incision of recently killed animals. In some large phocids, it is possible to collect milk surreptitiously from one nipple while the pup suckles on the other (Stull et al., 1967; Kooyman and Drabek, 1968; Riedman and Ortiz, 1979). Disadvantages to various procedures vary, and include potential postmortem changes due to loss of mammary metabolic function, contamination with blood and lipids of blubber origin during incision, contamination with dried salts or dirt on the

TABLE VII
Comparison of Mammary Milk Samples (M) to Gastric Contents (G) of Suckling Pups in Three Pinniped Species^a

Lactation stage (days PP)	Samples analyzed		Dry matter (%)		Fat (%)		Crude protein (%)		Gross energy ^b (kcal/g)	
	M	G	M	G	M	G	M	G	M	G
0-60	21	27	41.1	33.6	California sea lion ^c					
					31.7	21.9	9.8	8.9	3.46	2.52
90-120	12	9	54.2	43.5	43.7	32.4	9.6	8.9	4.54	3.47
1-30	19	8	---	---	Galapagos fur seal ^d					
					29.4	23.8	12.1	10.9	3.39	2.81
~3	5	6	56.3	44.8	Harp seal ^e					
					44.7	34.2	8.1	6.8	4.55	3.51
~8	6	6	61.5	51.4	49.2	39.3	7.9	6.4	4.94	3.96
~11	3	3	67.6	57.8	57.1	42.9	7.7	6.9	5.65	4.31

^aData are mean values; days PP, days postpartum.
^bGross energy calculated as (fat × 9.11 + protein × 5.86)/100 (Ofteidal, 1984a).
^cO. T. Ofteidal, D. J. Boness, and S. J. Iverson (unpublished); milk samples from immobilized females; gastric samples collected directly after observed suckling.
^dTrillmich and Lechner (1986).
^eO. T. Ofteidal, D. J. Boness, and W. D. Bowen (unpublished); milk samples from immobilized and shot females; gastric samples from suckling pups.

nipple or surrounding pelage, and inability to obtain large samples due to time constraints associated with immobilization procedures.

Among many domestic and terrestrial mammals, the fat content of milk rises progressively over the course of mammary evacuation such that the final fraction may be severalfold higher in fat content than the first fraction obtained (Oftedal, 1984a). Data for hooded seals, harp seals, and California sea lions do not show a significant increase in the fat content of sequential samples other than a small rise (from 32 to 34% fat) in the California sea lion in the first week postpartum (O. T. Oftedal, D. J. Boness, and W. D. Bowen, unpublished; O. T. Oftedal, D. J. Boness, and S. J. Iverson, unpublished). Nonetheless, it is probably prudent during milk collection to evacuate the mammary gland as completely as conditions permit.

In many pinniped studies, only one or a few samples of milk have been analyzed (Table VI), yet a few samples may not be representative. In California sea lions considerable variation can occur among samples collected from different teats of the same animal. The great differences in levels of dry matter (32–54%) and fat (19–44%) among teats of an animal that had recently given birth may reflect which teats had been suckled and to what extent (O. T. Oftedal, D. J. Boness, and S. J. Iverson, unpublished). Later in lactation interteat variation appears to be less, although aberrant samples may result from mastitis or involution processes in a gland that fails to be suckled.

The use of exogenous oxytocin facilitates milk collection in pinnipeds, presumably by initiating the milk ejection reflex. In some domestic animals the use of repeated, large doses or continuous infusion of oxytocin may reduce milk lactose content and alter electrolyte ratios, probably through effects on intercellular junctions in the mammary alveoli (Linzell et al., 1975). Because alveolar milk is apt to constitute but a small fraction of the milk collected in pinniped studies, the effects on milk composition of single oxytocin doses are probably negligible. In hooded and harp seals, milk samples obtained after oxytocin administration are similar in gross composition to samples obtained immediately postmortem (O. T. Oftedal, D. J. Boness, and W. D. Bowen, unpublished).

3.1.2. Lactation Stage

Milk composition changes markedly through the course of lactation in some pinniped species. Most notable is the enormous increase in fat content from about 10% at birth to about 50% at 2 weeks in southern (Bryden, 1968; Peaker and Goode, 1978) and northern elephant seals

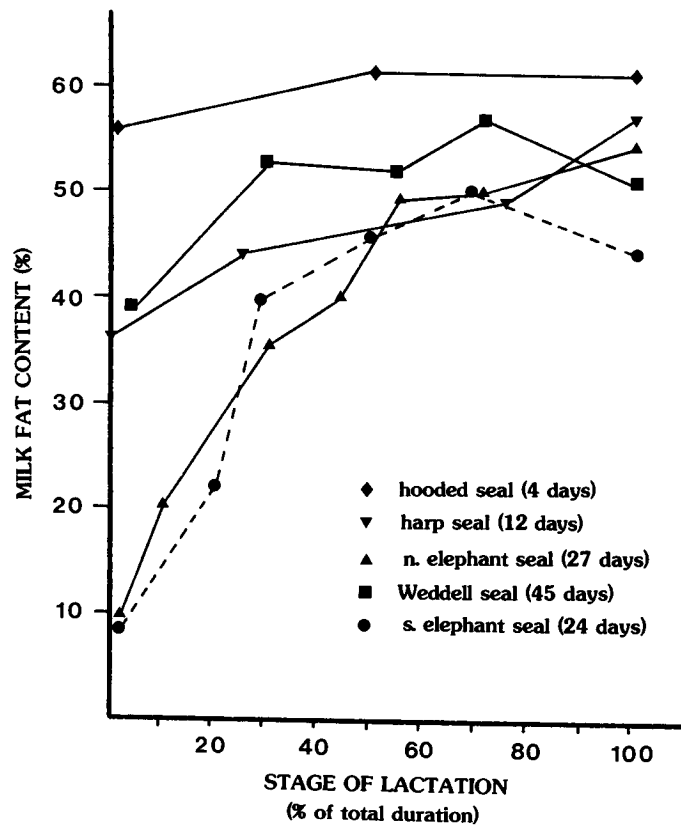


FIGURE 4. The relationship of milk fat content to stage of lactation in phocids. Each point represents a mean value at that stage. The number of samples analyzed for each species are as follows: hooded seal, $n = 22$; harp seal, $n = 19$; southern elephant seal, $n = 12$; northern elephant seal, $n = 44$; Weddell seal, $n = 11$. References as in Table VIII.

(Riedman and Ortiz, 1979) (Fig. 4). Protein content shows no change or a slight decline in this period. Thereafter samples exhibit variability in composition, but no consistent trends in either fat or protein content. The decline in fat and protein content beyond 2 weeks postpartum observed by Bryden (1968) was probably an artifact of the small number of samples ($n = 2$). Peaker and Goode (1978) did not confirm this trend (Fig. 4).

A similar but less pronounced rise in fat content in the first few weeks postpartum is found in both Weddell seals (Stull et al., 1967;

Kooyman and Drabek, 1968; Tedman, 1980) and harp seals (O. T. Oftedal, D. J. Boness, and W. D. Bowen, unpublished). (Fig. 4). In these species milk dry matter content tracks fat content, but is about 10–15% higher. In harp seals crude protein content of milk is significantly higher at birth (10.3%, $n = 5$) than at subsequent sampling times (7.9%, $n = 14$) (O. T. Oftedal, D. J. Boness, and W. D. Bowen, unpublished), but the relatively few samples of Weddell seal milk analyzed reveal no consistent trend (Tedman, 1980). The hooded seal exhibits little change in milk composition during its 4-day lactation period ($n = 22$ samples) (Fig. 4). Crude protein content declines from 6.2% at birth to 4.9% at 2–4 days, but no trends are apparent in dry matter or fat (O. T. Oftedal, D. J. Boness, and W. D. Bowen, unpublished).

Compositional trends during lactation are not as well documented for otariids. Milk of the South American fur seal increases in fat content from 31% in the first month postpartum to 44% in the fifth month and further to 55% in the 10–11th months. Dry matter follows a parallel trend (46, 54, and 68% in the first, fifth, and 10–11th months, respectively), but protein level averages 10–12% throughout (Ponce de Leon, 1984). Trends in California sea lions are remarkably similar in the first half of lactation. Fat increases from 32% at 0–2 months to 44% by the fourth month after birth, whereas dry matter rises from 41 to 54%. Protein content remains at about 9–10% over this period (Oftedal et al., 1983).

In the northern fur seal, it appears that milk fat content decreases somewhat during the initial postpartum period before females depart on feeding trips. Costa and Gentry (1986) report a decline in fat content from 46 to 40% in the first 8 days after birth. Data available from other laboratories are consistent with this trend, but the absolute fat values on the day of birth (58.7%, $n = 2$), at 1 day postpartum (52.9%, $n = 2$), and for the period of 10 days to 2 months (48.8%, $n = 6$) are considerably higher (Ashworth et al., 1966; Fay, 1982, personal communication; Dosako et al., 1983). According to Costa and Gentry (1986), the initial fat decline is followed by a gradual increase in average fat level such that by 2 months the fat content of northern fur seal milk is comparable to that at birth. California sea lion milk at 2 months postpartum is not significantly different in fat from that at birth (Oftedal et al., 1983), but trends in the interim have not been examined. In the Galapagos fur seal, milk fat content is reported to decrease by 7 percentage points during the first month, whereas crude protein remains unchanged (Trillmich and Lechner, 1986).

In otariids, time of sampling relative to female arrival and departure on feeding cycles may have an effect on milk fat content. Milk obtained

from northern fur seals on arrival is on average 6 percentage points higher in fat content than milk collected just prior to departure (Costa and Gentry, 1986). Comparable data are not available for other species. Northern fur seals may represent an extreme case, since periods of absence are longer than in other otariids (Table V). Some of the discrepancy in reported fat values for northern fur seal milk may stem from sampling procedures; incomplete fat extraction due to problems with analytical methodology may also be involved.

Data on milk composition in the last half of lactation are scanty for most otariids. Single samples of late-lactation milk have been assayed for both the California sea lion (Pilson and Kelly, 1962) and northern fur seal (Ashworth et al., 1966). The variability of fat content among samples implies that single samples may not be good indicators of trends.

3.1.3. Interspecies Variation at Mid- to Late Lactation

Given the effects of lactation stage on milk composition, direct interspecies comparisons are valid only at equivalent lactation stages. Comparisons among terrestrial mammals usually focus on midlactation, which may be defined as the period about peak lactation during which milk composition is relatively constant (Oftedal, 1984a). The timing of peak lactation in pinnipeds is not known, but constancy in milk composition is typically reached in phocids in the middle or latter part of lactation (Fig. 4). Milk composition data for this time period are available for two otariids and five phocids (Table VIII).

At this lactation stage the milks of all studied pinnipeds are remarkably similar in dry matter, fat, protein, sugar, and gross energy (Table VIII). Five species (northern fur, South American fur, harp, Weddell, and northern elephant seals) produce milks that are very similar: 63–68% dry matter, 51–55% fat, 8–11% protein, trace levels of sugar, and 5.2–5.7 kcal gross energy per gram. The lower values of dry matter, fat, and energy in the California sea lion (Table VIII) are for samples from the first half of lactation, and may not be representative of subsequent secretion. The similarity in compositional changes for milks of South American fur seals and California sea lions (see Section 3.1.2) suggest that late-lactation milk of California sea lions may be comparable to the five species listed above. The difference between northern and southern elephant seals may be an artifact of small sample numbers, because the trends in milk composition over the first few weeks are so similar (Fig. 4).

TABLE VIII
Milk Composition at Mid- to Late Lactation among Pinnipeds^a

Species (lactation duration, days)	Lactation stage		Dry matter (%)	Fat (%)	Crude protein (%)	Sugar (%)	Gross energy ^b (kcal/g)	References
	Days PP	n						
Phocids								
Hooded seal (4)	2-4	15	69.7	61.4	4.9	—	5.88	O. T. Oftedal, D. J. Boness, and W. D. Bowen (unpublished)
Harp seal (12)	~8-12	9	63.5	51.8	7.8	—	5.18	O. T. Oftedal, D. J. Boness, and W. D. Bowen (unpublished)
Southern elephant seal (23)	11-26	5	—	46.9	7.4	0.03	4.71	Peaker and Goode (1978) ^d
Northern elephant seal (27)	14-28	9	67.2	54.4	9.0	<0.25	5.48	Riedman and Ortiz (1979)
Weddell seal (45)	10-43	7	66.2	53.6	8.9	0.0	5.40	Tedman (1980)
Otariids								
Northern fur seal (120)	30-120	5	63.3	50.7	10.3	0.1	5.20	Ashworth et al. (1966), Dosako et al. (1983)
California sea lion ^e (~300)	90-120	12	54.2	43.7	8.9	0.6	4.50	O. T. Oftedal, D. J. Boness, and S. J. Iverson (unpublished)
South American fur seal (~365+)	270-330	5	67.9	55.2	11.6	0.0	5.71	Ponce de Leon (1984)

^aData are mean values.

^bGross energy calculated as (fat% × 9.11 + protein% × 5.86)/100 (Ofstedal, 1984a).

^cResults probably do not represent late lactation (see text).

^dSpecies incorrectly identified as Antarctic fur seal (see Bonner, 1984; M. Peaker, personal communication).

It has been suggested that otariids produce more dilute milk than phocids (Laws, 1959; Bonner, 1984) and that the fat content of otariid milk is correlated to the length of time the mother is away on feeding trips (Gentry et al., 1986; Trillmich and Lechner, 1986). While many reports for otariids do indicate rather low dry matter and fat values, most of these reports are based on milk samples taken in the first half of lactation (for example, Pilson and Kelly 1962; Fay, 1982; Oftedal et al., 1983; Costa and Gentry, 1986; Trillmich and Lechner, 1986) or gastric samples (Rand, 1955; Bonner, 1968). Available information of milk samples from mid-late lactation (Table VIII) do not support hypotheses of a difference between otariids and phocids, or of a correlation to feeding cycle duration in otariids. As more complete information is obtained for additional species, it may become possible to correlate the profound differences in fat content in early lactation to behavioral or physiological parameters. It is intriguing, for example, that both the phocid (hooded seal) and the otariid (northern fur seal) with the highest known fat content in early lactation are species with especially short lactation periods.

Relative to other mammals, pinnipeds secrete milk that is very energy-dense (4.5–5.9 kcal/g at mid- to late lactation). Energy densities above 3.5 kcal/g are found only in some bears in late lactation (Jenness et al., 1972) and in some cetaceans (Jenness and Sloan, 1970). Hooded seals produce the most highly energy-rich milk that has been reported for any mammalian species (Table VIII).

Various hypotheses have been put forth to explain the adaptive significance of the characteristically high fat and energy content of pinniped milks. High fat content is accompanied by low water content. In phocids that fast during relatively long lactation periods (for example, elephant and Weddell seals, Table II), low milk water content may be important to maternal water balance. In species with a very abbreviated lactation period (for example, the hooded seal, Table II), high fat content may facilitate the rapid transfer of fat and energy to pups as needed for rapid postnatal blubber deposition. In otariids, high-energy-density milks are associated with relatively low volumes of secretion (see Table XIII) and may relate to the finite capacity of the mammary glands as storage organs during foraging trips. Mammals with long intersuckling intervals typically produce concentrated milks (Oftedal, 1984a).

Protein accounts for about 12% of milk energy in the California sea lion, South American fur seal, and northern fur seal, 9–10% in the harp seal, Weddell seal, and the two elephant seals, and 5% in the hooded seal. These values are all low relative to typical values of 20–35%

for most terrestrial mammals, but are comparable to primate values of 7–17% (Oftedal, 1984a). Otariids, like primates (Payne and Wheeler, 1968), have slow growth rates relative to metabolic size; protein requirements should be low relative to energy needs. Although phocids gain mass rapidly after birth, much of this gain is energy-rich blubber rather than protein-containing tissue (Worthy and Lavigne, 1983b; Bowen et al., 1986b). Phocid pups have high fat needs rather than low protein requirements. The fact that the species with the greatest postnatal growth rate (hooded seal; Bowen et al., 1985) has the lowest percentage of milk energy as protein is consistent with this hypothesis.

3.2. Detailed Milk Constituents

3.2.1. Proteins

In most pinniped studies milk protein is calculated as total nitrogen $\times 6.38$. Because nonprotein nitrogen comprises about 3–7% of total nitrogen in milk of California sea lions, northern fur seals, and Galapagos fur seals (Ashworth et al., 1966; Oftedal, 1984a; Trillmich and Lechner, 1986), this calculation probably overestimates milk protein content by a small amount.

Milk proteins are characterized as caseins or whey proteins, depending on solubility at acid pH. Upon exposure to gastric acidity and proteases, casein micelles coalesce to form curds that erode slowly, releasing protein and peptides for further digestion in the duodenum. Casein micelles are considerably larger in northern fur seal milk than in bovine milk, and include five major casein components (Dosako et al., 1983). Caseins are reported to account for 44–72% of total protein in several species of phocids (Jenness and Sloan, 1970), and for 52% in the northern fur seal (Ashworth et al., 1966).

Little work has been done on whey proteins of pinniped milks. Gel electrophoresis of whey proteins from northern fur seal milk revealed a prominent band corresponding in mobility to β -lactoglobulin; other minor bands were also observed (Dosako et al., 1983). Southern elephant seal milk contains a whey protein with the electrophoretic mobility of serum albumin (Shaughnessy, 1974). α -Lactalbumin levels are very low or undetectable in California sea lion and northern fur seal milks (Schmidt et al., 1971; Johnson et al., 1972). Pinniped milks undoubtedly contain enzymes and other proteins found in milks of other mammals. High activity of bile salt-stimulated lipase has recently been demonstrated in hooded seal milk (Freed et al., 1986).

Amino acid analyses of total protein, casein, and/or whey protein

fractions have been published for northern fur seal and harp seal milks (Ashworth et al., 1966; Lauer and Baker, 1977; Dosako et al., 1983).

3.2.2. Lipid Constituents

Milk fat consists of various lipid classes. Triglycerides account for about 98–99% of the lipids in California sea lion milk (J. Bitman, D. L. Wood, S. J. Iverson, and O. T. Oftedal, unpublished). Other neutral lipid classes include diglycerides (1% or less of total lipids), monoglycerides (0.1–0.2%), free fatty acids (0.2–0.6%), and cholesterol (0.3%). Phospholipids account for about 0.5% of the total lipids. The patterns in other pinnipeds are probably similar.

Fatty acid constituents of the neutral lipids have been determined for seven species of pinnipeds (Tables IX and X). Methods for chromatographic isolation and identification of medium to moderately long-chain fatty acids (C_{14} – C_{18}) are well established. Oleic (18:1), palmitic (16:0), and palmitoleic (16:1) are predominant, although their relative contributions vary among species (Table IX). Pinniped milks are also very rich in long-chain, polyunsaturated fatty acids that exhibit prolonged retention times on gas-liquid chromatography (GLC) columns (Table X). Fatty acids with retentions equivalent to or greater than linolenic acid (18:3) account for 20–42% by weight of the total fatty acids. Investigators have assigned different identities to the major GLC peaks, even for the same species (Table X). Both the resolution and the assigned identities of these peaks may be questioned, given the limitations of methodology in the 1960s, when most of these analyses were conducted. Further investigation and identification of the very long-chain fatty acids of pinniped milks are needed using currently available capillary column methods and appropriate standards.

In pinnipeds, milk fatty acids are probably derived with little modification from dietary organisms such as plankton and fish (Ashworth et al., 1966; Stull et al., 1967; Van Horn and Baker, 1971) and may therefore reflect differences in fatty acid composition of diets. The proportions of component fatty acids of blubber vary among species, locality, stage of lactation, fasting state, and location on the body (Meara, 1952; Bryden and Stokes, 1969; Jangaard and Ke, 1968). Some of these factors may also influence milk fatty acid patterns, especially when milk lipids must be mobilized from blubber stores.

3.2.3. Carbohydrates

Pinniped milks contain very low levels of carbohydrate (Table VIII). Although lactose is the predominant sugar in milks of many mammals,

TABLE IX
Predominant Medium- to Long-Chain Fatty Acids in Pinniped Milks

Species	n	Percentage by weight ^a						References
		14:0	16:0	16:1	18:0	18:1	18:2	
				Phocids				
Grey seal	1-2	3.0	17.2	14.3	1.8	30.6	0.6	Meara (1952), Ackman and Burgher (1963)
Harp seal	10	4.9	11.8	19.9	4.2	23.5	1.7	Jangaard and Ke (1968), Glass and Jenness (1971), Cook and Baker (1969), Van Horn and Baker (1971)
Hooded seal	1	3.6	9.5	13.5	2.8	27.2	1.3	Jangaard and Ke (1968)
Northern elephant seal	30	2.6	16.8	7.0	3.7	44.1	1.9	Glass and Jenness (1971), Riedman and Ortiz (1979)
Weddell seal	15	9.8	14.7	12.4	1.8	39.0	2.3	Glass et al. (1967), Stull et al. (1967), Tedman (1980)
				Otarids				
California sea lion	2	5.9	17.8	6.8	3.9	17.4	2.0	J. Bitman, D. L. Wood, S. J. Iverson, and O. T. Oftedal (unpublished)
Northern fur seal	3	6.3	19.3	9.9	2.0	31.6	2.7	Ashworth et al. (1966), Glass et al. (1967), Dosako et al. (1983)

^aColumn headings identify fatty acid chain length and number of double bonds.

TABLE X
Identification of Major Long-Chain Fatty Acids in Pinniped Milks That Exhibit Prolonged Retention Times on Gas-Liquid Chromatography Columns

Species	Percentage by weight ^a								References
	Total ^b >18:2	20:1	20:4	20:5	22:1	22:5	22:6	Other majors ^c	
Grey seal	28.3	2.7	1.8	8.8	0.5	3.5	8.1	—	Ackman and Burgher (1963)
Harp seal	41.6	13.9	1.1	9.0	5.2	3.4	6.5	—	Jangaard and Ke (1968)
	28.6	11.7	0.9?	4.3	4.4	1.5	2.5	—	Cook and Baker (1969)
	31.8	8.3	0.8?	0.5	9.5	6.2	—	24:1	Van Horn and Baker (1971)
Hooded seal	36.7	15.0	1.6	6.8	5.0	1.7	3.9	—	Jangaard and Ke (1968)
Northern elephant seal	24.7	12.6	3.4	2.6	—	0.9	4.3	—	Riedman and Ortiz (1979)
Weddell seal	20.2	6.9	0.2	4.7	1.5	1.0	4.0	—	Stull et al. (1967)
California sea lion	41.7	4.4	2.4	7.7	3.0	3.0	15.9	—	J. Bitman, D. L. Wood, S. J. Iverson, and O. T. Oftedal (unpublished)
Northern fur seal	32.1	4.1	—	—	5.4	—	—	18:3, 22:2	Ashworth et al. (1966)
	22.1	6.8	2.4	4.8	1.0	1.5	3.7	—	Dosako et al. (1983)

^aColumn headings identify fatty acid chain length and number of double bonds.
^bCombined weight percentage of all fatty acids with retention times greater than that of 18:2.
^cIncludes other long-chain, unsaturated fatty acids present at levels greater than 2.0% by weight.

many pinniped milks are either devoid of lactose or contain insignificant amounts (Pilson and Kelly, 1962; Kerry and Messer, 1968; Johnson, 1975). Indirect calculation of milk carbohydrate content by subtracting fat, protein, and ash from dry matter level is apt to overestimate true carbohydrate content (R. E. A. Stewart et al., 1983) and is responsible for some erroneous values (for example, Amoroso et al., 1951; Lavigne et al., 1982). Myoinositol, a carbohydrate with vitaminlike activity in a few mammalian species (Cody, 1984), has been found at high concentration (0.12%) in northern fur seal milk (Dosako et al., 1983) and is probably present in southern elephant seal milk (Peaker and Goode, 1978).

3.2.4. Minerals

In the milks of terrestrial mammals calcium and phosphorus are usually present in a weight ratio of about 1.6:1 (Jenness, 1979), similar to estimated requirements of 1:1 to 2:1 in most species. By contrast, inverse Ca/P ratios of 0.5:1 to 0.9:1 have been reported for California sea lions, northern fur seals, harp seals, and northern elephant seals (Table XI). In California sea lions, phosphorus levels are apparently low in the immediate postpartum period, such that the Ca/P ratio may be as high as 2.8:1 (Table XI), but this ratio inverts by the second month after birth. The adaptive significance of an inverse Ca/P ratio is not clear. Jenness (1979) noted that pinnipeds had much less calcium and phosphorus in milk than would be predicted based on casein content.

Sodium (Na), potassium (K), and chloride (Cl) are predominantly present in ionic form in the aqueous phase of milk. In most species the isosmotic condition of milk relative to blood is maintained by the interplay of lactose and mineral ions in controlling the flow of water into mammary secretory cells and alveolar lumina (Peaker, 1977). The virtual absence of lactose from pinniped milks suggests that secretory mechanisms may operate differently in controlling secretion of the aqueous phase. The ratio of potassium to sodium should be similar to that of intracellular fluids, about 3:1 on a molar basis or 5:1 on a weight basis, and this is in fact observed in many species (Peaker, 1977). Data on pinniped milks indicate that the weight ratio of K/Na is much lower, about 1.0–2.4 (Table XI). It is difficult to collect milk by mammary expression in pinnipeds without potential contamination from dried salts (especially sodium) on the teat, skin, and pelage. This may explain the particularly high sodium levels (800–1000 mg/kg) and low K/Na ratios (0.7–1.0) reported by Riedman and Ortiz (1979) for northern elephant seal milk (Table XI). In California sea lions, prewashing of the

TABLE XI
Major Minerals in Pinniped Milks^a

Species ^b	Lactation stage (days PP)	n	mg/kg			Ca/P	mg/kg			K/Na	References
			Ca	P	Phocids		K	Na			
Harp seal Northern elephant seal	2-6	4	723	1200	0.60	1084	618	1.8	Van Horn and Baker (1971)		
	?	7	511	939	0.54	—	—	—	R. Jenness (personal communication)		
	0-7	5	—	—	—	1060	1020	1.0	Riedman and Ortiz (1979)		
	8-14	9	—	—	—	820	990	0.8	Riedman and Ortiz (1979)		
	15-21	10	—	—	—	720	770	0.9	Riedman and Ortiz (1979)		
	22-28	12	—	—	—	560	860	0.7	Riedman and Ortiz (1979)		
Southern elephant seal Weddell seal	21-28	4	—	—	—	1000	670	1.5	LeBoeuf and Ortiz (1977)		
	5-17	9	—	—	—	1360	990	1.6	Peaker and Goode (1978)		
	15-43	5	—	—	—	570	530	1.1	Tedman (1980)		
					Otariids						
California sea lion	<7	3	520	187	2.8	2400	1210	2.0	M. E. Allen, O. T. Oftedal, and D. J. Boness (unpublished)		
	30-60	4	885	1003	0.88	2030	1060	1.9	M. E. Allen, O. T. Oftedal, and D. J. Boness (unpublished)		
Northern fur seal Galapagos fur seal	90-120	3	683	1060	0.64	1620	670	2.4	M. E. Allen, O. T. Oftedal, and D. J. Boness (unpublished)		
	30-60	1	567	1193	0.48	838	521	1.6	Dosako et al. (1983)		
	1-30	17	630	—	—	1670	—	—	Trillmich and Lechner (1986)		

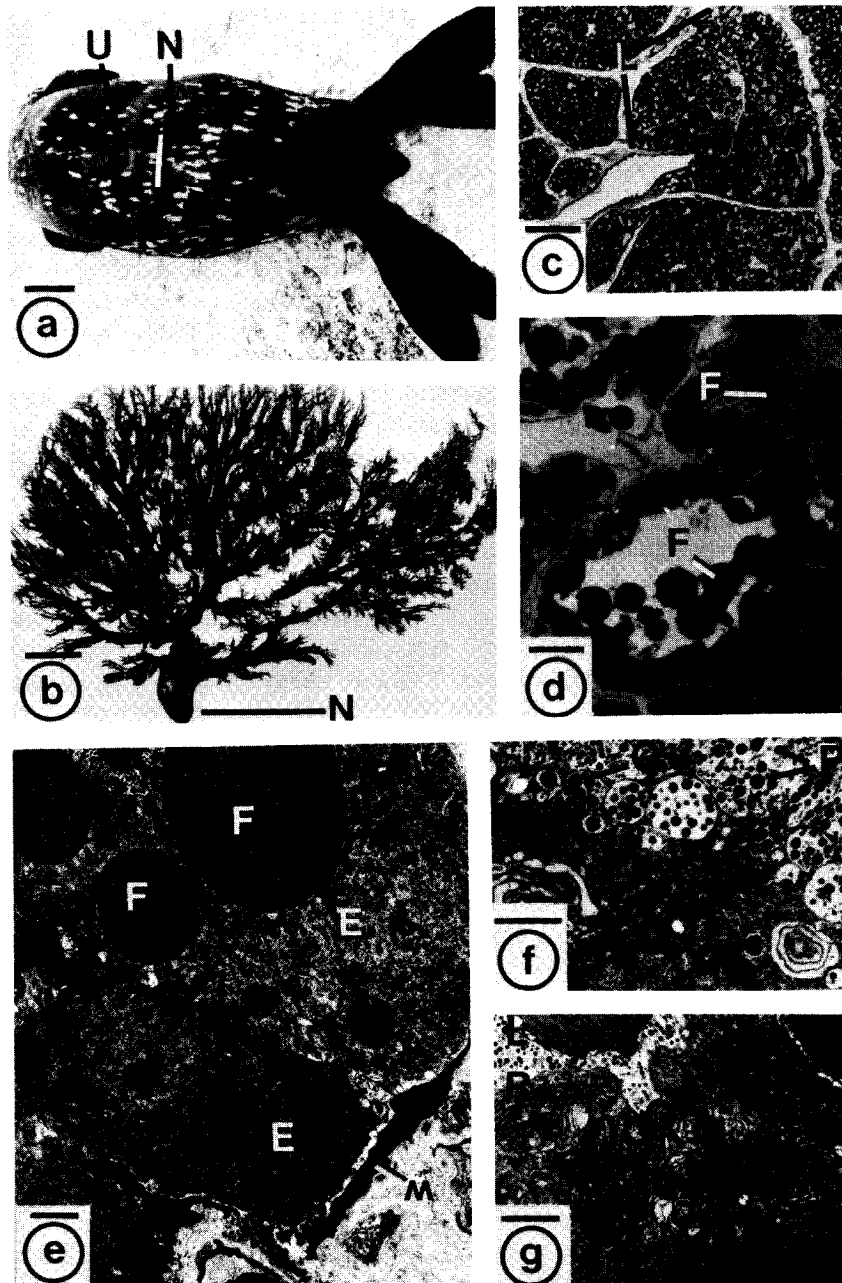
^aColumn headings refer to calcium (Ca), phosphorus (P), potassium (K), and sodium (Na).
^bAll available sources included, except Cook and Baker (1969), which contains analyses in disagreement with subsequent reports from the same laboratory, and is apparently erroneous.

teat area with distilled water and collection of large volumes may have reduced contamination, as evidenced by the higher K/Na ratio (Table XI). Alternatively, interspecies differences in K/Na ratios may occur.

Peaker and Goode (1978) reported that southern elephant seal milk was somewhat hyperosmotic to blood, and Tedman (1980) found rather high osmolality in four of five samples of Weddell seal milk. Possible effects of freezing of samples and salt contamination cannot be ruled out, however. The osmolality of the aqueous phase of a sample of California sea lion milk that was measured shortly after collection and had not been frozen was 286 mosm/kg (M. E. Allen, O. T. Oftedal, and D. J. Boness, unpublished results), well within the expected range for fluids isoosmotic to blood. Further study of the osmolality of pinniped milks is needed.

Because chloride is found almost entirely in the aqueous phase, chloride data can be extrapolated to a whole-milk basis by dividing by milk water content. Chloride concentrations in milks of the northern fur seal, southern elephant seal, and Weddell seal average about 1000–1300 mg/kg (Ashworth et al., 1966; Peaker and Goode, 1978; Tedman, 1980; Dosako et al., 1983). Milk magnesium levels average about 120–170 mg/kg in California sea lions, northern fur seals, and harp seals (Van Horn and Baker, 1971; Dosako et al., 1983; M. E. Allen, O. T. Oftedal, and D. J. Boness, unpublished results). Iron, copper, zinc, and selenium were measured at levels averaging 5.4, 2.6, 7.7, and 0.45 mg/kg in California sea lion milk (D. Allen, O. T. Oftedal, and D. J. Boness, unpublished results, $n = 12$); roughly similar levels have been reported for northern fur seals (Dosako et al., 1983). The extent to which minor contamination may have affected trace mineral levels cannot be ascertained.

FIGURE 5. Mammary anatomy and ultrastructure in the lactating Weddell seal. (a) Adult female, showing location of semiprotruded nipples (N) near umbilicus (U); (bar = 20 cm). (b) Resin cast of milk duct system or mammary gland (N = nipple; bar = 3 cm). (c) Mammary tissue showing a lobule (L) filled with alveoli (hematoxylin and eosin; bar = 400 μ m). (d) Mammary tissue showing an alveolus with fat droplets (F) (toluidine blue stain; bar = 20 μ m). (e) Electron micrograph of alveolar epithelium showing myoepithelial cells (M), epithelial cells (E), and fat droplets (F); (bar = 2.0 μ m). (f) Electron micrograph of a secretory epithelial cell showing Golgi vesicles (GV) and protein micelles (P) in the lumen; (bar = 1.0 μ m). (g) Electron micrograph of a secretory epithelial cell showing Golgi apparatus (G), rough endoplasmic reticulum (R), and lumen (L); (bar = 2.0 μ m).



4. MAMMARY ANATOMY AND FUNCTION

4.1. Gross Anatomy

The otariids and odobenids possess four mammary teats (nipples) located on the ventral abdominal wall anterior and posterior to the umbilicus (King, 1983). The bearded seal (Mansfield, 1967) and the monk seal (Kenyon and Rice, 1959; King, 1983) also possess four teats, whereas all other phocids have two abdominal teats adjacent to or posterior to the umbilicus (King, 1983) (Fig. 5a). Supernumerary teats have been reported in southern elephant seals (Laws, 1956), the northern fur seal (Scheffer, 1962), and the walrus (J. King, personal communication). The nipples are eversible under the influence of a sucking pup (Amoroso and Matthews, 1952), retracting below the general body level to be hidden by the pelage when sucking ends. In the Weddell seal the nipples protrude about 3.7 cm beyond the general body contour during nursing (Bertram, 1940). In some species, nipples may remain everted during off-teat intervals and continue to squirt milk (Fig. 1).

Information suggests that the mammary glands differ in shape and size between phocids and otariids. In phocids such as the harbor seal (Harrison, 1969), southern elephant seal (Laws, 1956; Bryden, 1968), and Weddell seal (Bertram, 1940; Tedman, 1977) the mammary glands form two flattened ellipsoid glands beneath the subcutaneous fat on the abdomen. In the northern fur seal the mammary glands spread like an extensive apron over the lower thorax, abdomen, and sides of the body (Scheffer, 1962). In all pinnipeds the mammary glands follow the general contour of the body and are not normally visible externally. However, in Weddell seals maternal fat loss becomes so marked near weaning that outlines of the mammary glands are often visible (Tedman, 1980). There have been no detailed descriptions of the mammary glands of otariids or odobenids. Most of our knowledge of pinniped mammary anatomy comes from observations on a few species of phocids.

The dimensions of lactating mammary glands have been measured following dissection in several species. The size of the gland depends on the size of the cow and on the time elapsed since the pup last sucked (Laws, 1956). In the Falkland Islands, for example, lactating mammary glands of a large southern elephant seal cow may be up to 82.5 cm long, 25 cm wide, and 11.2 cm thick, but only 57.5 by 20 by 7.5 cm in an average-sized cow ($n = 10$) (Laws, 1956). Laws estimated gland volume from these dimensions and concluded that volumes range from 2.0 to 5.3 liters. At Macquarie Island, estimated volumes for this species are

similar, but somewhat smaller, 0.9–4.5 liters (Bryden, 1968). In Weddell seals lactating mammary glands may be up to 45 by 22.5 by 10 cm, with estimated volumes of 1.4–5.3 liters (Bertram, 1940; Tedman and Bryden, 1981a). Grey seal mammary glands are about 50 cm in length and 5 cm thick (Harrison, 1969), whereas hooded seal glands are about 78 cm long and 21 cm wide (W. D. Bowen, D. J. Boness, and O. T. Oftedal, unpublished, $n = 2$). Scheffer (1962) reports that mammary glands of the northern fur seal can be 60 cm long and 50 cm wide, with a depth of 1–2 cm. Given the small size of this otariid, the mammary surface area (up to 2190 cm²; Scheffer, 1962) is remarkable. Scheffer (1962) suggests that mammary capacity may be 2–3 liters. Weight gains of lactating northern fur seals during foraging trips are of a similar magnitude (about 3–4 kg; Costa and Gentry, 1986) and may largely represent mammary filling at sea.

Among terrestrial mammals, interspecies differences in mammary tissue weight are related to body weight by an allometric equation (Hanwell and Peaker, 1977):

$$Y = 0.045(\text{body weight in kg})^{0.82}$$

Unfortunately, little is known of mammary weights in pinnipeds. Tedman (1985) reported a weight of 4 kg for an apparently normal mammary gland of a lactating Weddell seal. The combined weight of 8 kg is somewhat greater than the 6.1–6.7 kg predicted for a 400- to 450-kg female from the allometric equation. In hooded seals the discrepancy is even greater: a 166-kg female with a pup near weaning had a combined mammary weight of 5.7 kg, nearly twice the predicted value of 3.0 kg (W. D. Bowen, D. J. Boness, and O. T. Oftedal, unpublished). Further data are required to determine if pinnipeds typically have large mammary glands relative to body weight.

The milk duct system of the mammary glands of the Weddell seal and southern elephant seal resembles that found in other eutherians in functioning as a series of reservoirs for milk storage between and during suckling periods (Tedman and Bryden, 1981b). In adapting to the flattened nature of the mammary glands, there is a radiating arrangement of large canals running parallel to the skin surface and draining more or less straight to a gland cistern deep to the nipple (Tedman and Bryden, 1981b) (Fig. 5b). While the milk duct systems of nonlactating and lactating glands are similar, the increased thickness of lactating glands results from the development of alveoli, terminal ducts, and fine collecting ducts (Tedman and Bryden, 1981a). Laws (1956) reported a

“small ampulla” beneath each nipple in the southern elephant seal and Murie (1874) found a “long capacious duct” deep to each of four teats in an adult male Steller sea lion.

4.2. Microscopic Anatomy

The histological appearance of nonlactating mammary glands of harp and hooded seals (Belov, 1971), southern elephant seals (Bryden and Tedman, 1974), and Weddell seals (Tedman and Bryden, 1981a) resembles that of glands at similar stages in other mammals (see review by Hollmann, 1974).

Mammary glands of newborn male and female harbor seals consist of ducts ending in tufts of short glands with no lumen and show no signs of being affected by the stimulus that causes marked change in the genital tract and associated glands at this time (Harrison, 1960). Amoroso et al. (1965) found a similar arrangement of mammary tissue in 2- to 13-day-old grey seals, a stillborn California sea lion, and a near-term harbor seal. In the adult Weddell seal the nonlactating mammary gland consists of branched and unbranched cords of epithelial cells and tubules compacted into widely spaced lobules (Tedman and Bryden, 1981a). Within lactating tissue alveoli are compacted together as lobules separated by thin connective tissue septa (Fig. 5c).

Alveoli possess a lumen bordered by a single layer of epithelial cells, which are surrounded by scattered myoepithelial cells (Tedman, 1980) (Fig. 5d). The mammary parenchyma shows a desynchronization of the secretory cycle, with alveoli varying from thin-walled units swollen with secretory products to thick-walled structures containing little secretion (Tedman, 1980).

According to Belov (1971), the mammary tissue from hooded seals displayed active liberation of secretion by the entire alveolar epithelium throughout lactation, with all alveoli distended and participating in a holocrine type of secretion. In this way functional cells are lost from the alveolar epithelium to be added to the secretory product. Belov claimed that harp seals also exhibit holocrine secretion, but that a desynchronization of secretory activity is indicated by the mixture of shrunken and distended alveoli observed in mammary tissue. The apparent synchronization of the cycle of secretory activity in mammary tissue of hooded seals led Belov to conclude that the mammary glands of this species function at a maximal level throughout the short nursing period. In the harp seal the secretory activity is less intense (desynchronization of secretory activity), but extended over a longer nursing

period. Belov (1971) believed that the nursing periods for hooded and harp seals were 10–12 and 21 days, respectively, but the true lactation lengths are closer to 4 and 12 days, respectively (Table II).

In all terrestrial mammals so far examined (Wooding, 1977) plus various cetaceans (van Utrecht, 1968), the Weddell seal (Tedman, 1983), and the southern elephant seal (Bryden and Tedman, 1974) there is no evidence of a holocrine method of secretion in mammary tissue. The mode of secretion of major milk constituents such as fat and protein seems to be identical in all mammals. It is unlikely that hooded or harp seals would be different. It is important to examine mammary tissue from these species at the electron microscopic level to substantiate the mode of secretion.

4.3. Ultrastructure and Secretory Processes

The mammary parenchyma in nonlactating and lactating Weddell seals is almost identical in ultrastructure to that found in other mammals (Tedman, 1983) (Figs. 5e–5g). Consistent with a high level of secretory activity, epithelial cells characteristically contain well-developed mitochondria, Golgi apparatus, rough endoplasmic reticula (RER), microvilli, and a labyrinth of irregular cytoplasmic processes from the basal plasma membrane (Tedman, 1980).

In mammary secretory cells in the Weddell seal, as in other mammalian species, milk protein appears as electron-dense granules (micelles) within vacuoles (vesicles) that are associated with the Golgi apparatus and scattered throughout the cytoplasm, especially in the apical region (Tedman, 1980) (Figs. 5f and 5g). In other mammals these vesicles have been shown to contain milk proteins, citrate, inorganic ions, lactose, and water (Wooding, 1977). The contents of these vesicles are released into the alveolar lumen by the process of exocytosis when the vesicles fuse with the apical plasma membrane.

In the Weddell seal the relative volumes of most organelles in secretory epithelial cells of the mammary gland are similar to those in other eutherians, but the relative volumes of RER and Golgi vacuoles are reduced (Tedman, 1983). While the significance of the reduced volume of RER is not clear, the decrease in relative volume and absolute diameter of Golgi vacuoles may be related to reduced lactose and water content of Weddell seal milk in comparison to terrestrial mammals for which comparable data are available, such as the rat. The osmotic movement of water into the Golgi vacuoles during lactose formation and subsequent transport to the apical cell surface is believed to be the main

mechanism by which bulk water movement into the milk occurs (Peaker, 1977). Consequently, the reduced volume of Golgi vacuoles in Weddell seal mammary tissue may reflect a relatively low rate of lactose synthesis and water transport compared to most terrestrial species.

However, Wooding (1977) concluded that there is no correlation between organelle content and gross milk composition in ten species of mammals, including a fur seal (species not identified). The values for relative volume of Golgi vesicles in the fur seal reported by Wooding (1977) were larger than those reported for the Weddell seal. Fur seal milk has even less lactose than Weddell seal milk. Mammary tissues from other pinniped species need to be examined to clarify this apparent anomaly.

In Weddell seal mammary tissue, fat droplets appear to be extruded from epithelial cells in the same manner as reported for numerous terrestrial mammals (Tedman, 1983). Fat droplets within mammary epithelial cells bulge into the apical plasma membrane and are ultimately extruded from the cell enveloped by a unit membrane derived from the apical plasma membrane and perhaps from Golgi vesicles associated with the lipid droplet (Mather and Keenan, 1983). The mode of secretion seems to fit the concept of an apocrine secretion in which there is loss of part of the secretory cell cytoplasm with the secretory product.

The fat droplets in milk samples, alveolar lumina, and epithelial cells have a larger mean diameter in Weddell seals than in other mammals that have been studied. Perhaps seals need to reduce the quantity of membrane required to package the large quantities of fat. The area of membrane per unit volume required to enclose fat droplets will be less for larger than for smaller droplets (Tedman, 1983). Golgi vacuoles fuse with apical plasma membranes during exocytosis and hence are believed to be responsible for replacement of apical plasma membrane lost during extrusion of fat droplets (Keenan et al., 1978). Reduced diameter and relative volume of Golgi vacuoles in Weddell seals will mean reduced membrane available for apical plasma membrane replacement.

However, according to Dylewski and Keenan (1983), there is evidence that most of the Golgi vesicular membrane material in bovine and rat epithelial cells may not be incorporated into apical plasma membrane. Rather, the Golgi vesicles fuse with each other, often forming vesicular chains of ten or more linked vesicles, of which only the terminal vesicle fuses with and becomes incorporated into the apical plasma membrane. The remaining linked vesicles disintegrate after the

vesicular contents are passed into the alveolar lumen. Consequently, fundamental concepts of the role of Golgi vesicular membrane or plasma membrane turnover need to be examined in mammary tissue of not only the Weddell seal, but all marine mammals where large quantities of fat are being secreted into the milk.

It remains unclear just how the pinniped mammary gland can produce milk with such a high fat content. Holt (1983) viewed the concentration of lipid droplets in milk as depending on their secretion rate in relation to the volume of the aqueous phase. An increased rate of fat synthesis and secretion accompanied by a reduced volume of the aqueous phase could produce an elevated fat content. More detailed work on pinniped mammary glands may expand our understanding of the flexibility that exists within the functional capabilities of mammary tissue in general.

4.4. Immunologic Function

Seals, like other carnivores, possess an endotheliochorial placentation (Sinha and Erickson, 1974). Hence, as in the dog and cat, there is probably some form of antibody transfer prenatally across the placenta, and postnatally via mammary gland secretions—the colostrum and milk (Brambell, 1970). The mammary gland provides passive immune protection to the suckling infant and participates in immunologic defence of its own tissues against infection by microorganisms (Watson, 1980). While these functions vary in importance in different species, there are no data available on immunity transfer in pinnipeds and hence there are many areas that need to be investigated.

Plasma cells secrete particular classes of immunoglobulins, especially IgA (Pumphrey, 1977), which may have an immunoprotective role within the lumen of the gut of the suckling young, acting against a variety of enteric microorganisms (Watson, 1980). Pumphrey examined the distribution of plasma cells within mammary tissue from the grey seal, harbor seal, southern sea lion, South American fur seal, and Antarctic fur seal as part of a review involving 60 species of mammals. The centrilobular distribution of plasma cells in the pinnipeds examined by Pumphrey was the same as that reported by him for man, rhesus monkey, dog, cat, cape buffalo, and whale. Fewer plasma cells were found in the mammary tissues of the fur seals than in harbor or grey seals, however. Pumphrey (1977) suggested that the unknown mechanism whereby fur seals avoid mammary involution during long feeding

trips away from the young might prevent the plasma cells from congregating in the mammary tissue of these animals.

4.5. Maintenance of Lactation and Mammary Involution

The maintenance of milk secretion by the mammary gland is dependent upon and controlled by various hormones, the most important in nonruminants being prolactin (Tindal, 1978). Prolactin is released by the pituitary gland in response to sucking or milking as well as other tactile stimuli, but the pattern of release and the quantities involved vary in different species (Tindal, 1978). The role of prolactin and other hormones in the control of lactation in pinnipeds is not known.

Despite the variation in suckling habits and the diversity in gross structure of mammary glands in different species, there seems to be a common mechanism of milk ejection for all mammals (Cross, 1977). The evacuation of milk is assisted by the contraction of myoepithelial cells, which surround secretory alveoli in a basketlike arrangement, under the influence of oxytocin released from the maternal neurohypophysis during suckling (Cross, 1977). Stimulation of the nipple during suckling provides the main afferent impulse for initiation of milk ejection, but in many species the sight or sound of the young or other features of the nursing routine may trigger milk ejection (Lincoln and Paisley, 1982).

Compression of alveoli following myoepithelial cell contraction forces the milk into various milk ducts where it is available for removal from the gland by the sucking of the young. In species such as ruminants where much of the milk is stored in voluminous cisterns, the milk ejection reflex is not essential for the feeding of the young, although it assists in moving the milk from the alveoli to the milk ducts (Lincoln and Paisley, 1982). However, in many species the storage capacity of the milk ducts is not large and the milk ejection reflex forms an important part of the process of milk removal by the sucking young.

The anatomic arrangement of the duct system of the mammary glands of the pinnipeds that have been studied suggests that these species should be largely dependent on the milk ejection reflex. The existence of a milk ejection reflex in pinnipeds is indicated by the presence of myoepithelial cells in the mammary alveoli of the Weddell seal (Tedman, 1983) and the observation that exogenous oxytocin injections assist in milk collection.

In all mammals studied a regular suckling stimulus is vital for maintenance of mammary gland function, and without it regression or

involution of the glandular tissue ensues (Cowie and Tindal, 1971). Involution follows a similar pattern in all species, but varies in duration. Removal of a sucking stimulus leads to milk accumulation, mammary gland distension, changes in milk composition, including a progressive increase in cellular content, and cellular degradation (Lascelles and Lee, 1978). Initial stages of cell degradation involving alterations to cell organelles occur within 1–3 days in a variety of mammals.

The mechanism whereby otariids avoid the onset of involution during the prolonged feeding trips at sea without exposure to suckling is unknown. It is possible that otariids reduce the effects of milk accumulation by combining a large storage volume with a relatively low rate of secretion of a high-nutrient-density milk. The extent to which mammary storage capacity in mammals is adapted to suckling interval is not known. Other mammals that suckle relatively infrequently produce concentrated milks (Oftedal, 1984a). The possibility that secretion rate varies between time on land and time at sea needs to be investigated. In mammals endogenous mammary factors such as prostaglandins and estradiol seem to play a significant role in the local control of the composition and rate of mammary secretion and may be particularly important (Maule Walker, 1984). The otariid mammary gland may prove to be a useful experimental model for understanding the physiological and biochemical regulation of milk secretion.

5. MILK PRODUCTION AND LACTATION ENERGETICS

5.1. Measurement of Milk Yield

Bryden (1968) made an early attempt to quantify milk production in the southern elephant seal on the basis of mammary volume, 12-h pup weight gains, and amounts of milk recovered from mammary glands and pup stomachs, but concluded that these estimates were not reliable. More accurate indirect estimates based on the energetics of maternal weight loss and pup weight gain have been published for the grey seal (Fedak and Anderson, 1982) and harp seal (R. E. A. Stewart and Lavigne, 1984). The applicability of isotope methods to pinnipeds under field conditions has led to a proliferation of milk production estimates in the past few years. Such data are now available for four phocids and two otariids (Tables XII and XIII).

The four phocids studied by isotope methods (Table XII) represent a wide range of lactation duration (4–45 days) and pup weight gain (about 2–6 kg/day). Interspecies comparison reveals a close correlation

TABLE XII
Milk Yields of Phocids Determined by Isotope Dilution Methods^a

Species (lactation duration, days)	Period of study ^b (days PP)	n	Initial female weight (kg)	Pup gain ^c (kg/day)	Daily milk yield (kg/day)	Yield		References
						per pup gain (kg/kg)	Yield as percent female weight	
Hooded seal (4)	0-4	7	179	5.71	8.52	1.55	4.8	O. T. Oftedal, D. J. Boness, and W. D. Bowen (unpublished observations)
Harp seal (12)	0-10	6	135	2.11	3.31	1.48	2.5	O. T. Oftedal, D. J. Boness, and W. D. Bowen (unpublished observations)
Northern elephant seal (27)	0-24	6	509	3.31	5.50	1.66	1.1	Costa et al. (1986); Ortiz et al. (1984)
Weddell seal (45)	8-38	9	447	1.98	3.54	1.96	1.0	Tedman and Green (1986)

^aValues are means unless otherwise indicated.
^bRange of pup ages over which isotope turnover measured; not all individuals were measured over the entire range.
^cMean growth rates for individual pups studied; species means may be somewhat different.
^dHooded seal data determined directly; data on other species calculated from mean daily yield and lactation duration.

TABLE XIII
Milk Yields of Otariids Determined by Isotope Dilution Methods^a

Species (lactation duration, days)	Period of study (days PP)	n	Female weight (kg)	Pup gain (kg/day)	Daily milk yield (kg/day)	Yield		References
						per pup gain (kg/kg)	Yield as percent female weight	
Northern fur seal (120) California sea lion (~300)	0-7	6	37.7	0.185	0.50	2.7	1.3	Costa and Gentry (1986) O. T. Oftedal, S. J. Iverson, and D. J. Boness (unpublished)
	10-60	13	37.7 ^b	0.065 ^c	0.450 ^d	6.9	1.2	
	0-30	22	88.1 ^e	0.121	0.70	5.8	0.8	
	30-60	13	88.1	0.124	0.73	6.3	0.8	
	90-120	5	88.1	0.085	1.01	11.9	1.1	

^aData are mean values.
^bAverage weight from perinatal period used, since subsequent weights not reported.
^cAverage weight gain of male and female pups, from Gentry et al. (1986).
^dCalculated using 8 days as the average duration from the beginning of one suckling period to the beginning of the next.
^eAverage of all lactating females weighed 0-120 days postpartum (n = 8).

of estimated mean daily milk yield to rate of pup weight gain ($r = 0.995$, d.f. = 2, $P < 0.01$). The ratio of mean milk yield to mean pup gain ranges from 1.5 to 2.0 in the species studied (Table XII). Daily milk yields are equivalent to about 1.0–1.1% of initial maternal weight in the two larger species with longer lactations (northern elephant seal, Weddell seal), in contrast to 2.5% in the harp seal and 4.8% in the hooded seal with shorter lactation periods. Because milk production derives entirely from maternal nutrient stores, the rate of depletion of stores is apparently greater in those species with short lactation periods.

Milk production has been measured over the period of birth to weaning in the hooded seal; in the other species isotope dilution measurements cover a large part of lactation and can be extrapolated to the entire period (Table XII). Total yields increase with lactation duration, from 27.6 kg in the hooded seal to 159 kg in the Weddell seal. These yields are equivalent to 15, 30, 29, and 36% of initial female weight in hooded, harp, northern elephant, and Weddell seals, respectively. Because lactating phocids consume little or no food or water, female weight losses during lactation can be expected to exceed the above percentages by an amount dependent on metabolic processes and evaporative and other water losses. Serial weighings of females throughout lactation indicate weight losses of 39 and 59% in northern elephant and Weddell seals (Costa et al., 1986; Tedman and Green, 1986).

Milk intake estimates in otariids are restricted to the first 2 months of lactation in the northern fur seal and the first 4 months in the California sea lion (Table XIII). Average daily yields are a similar percentage of maternal weight (0.8–1.3%) as in northern elephant seals and Weddell seals. The average yield includes days the mother is at sea foraging, such that the delivery rate to the pup during periods of suckling will be much higher. In the northern fur seal there is little change in level of production from the initial period of continual maternal presence to the subsequent phase of feeding cycles. In the California sea lion, milk production appears to rise somewhat from the second to the fourth month of lactation (Table XIII).

The ratio of milk yield to pup weight gain may be higher in otariids than in phocids, but because available data cover only a part of the lactation period for just two otariids, a quantitative comparison cannot be made. For both California sea lions and northern fur seals, the greater growth efficiency in early lactation compared to later stages may be related to the continuous availability of the mother before she begins her foraging trips (Table XIII). In the northern fur seal, the ratio of milk yield to pup growth (2.7) in early lactation is comparable to that of phocids (Table XII). During the second month postpartum, both species

ingest 6–7 kg milk per kg weight gain. The higher ratio (11.9) observed at 90–120 days in the California sea lion is probably age-related. In addition to the low growth rate in the five pups of this age used in the milk yield study, a similar decline in growth rate occurred in a larger sample of pups (D. J. Boness, O. T. Oftedal, and K. A. Ono, unpublished).

Milk delivery rates of 0.84, 2.82, and 6.48 kg/h nursing can be calculated for California sea lions, harp seals, and northern elephant seals, respectively, from data on daily yield (Tables XII and XIII) and cumulative time on teat (Table III). Absolute delivery rate appears to be a function of female size, but if delivery rate is expressed as a percentage of female weight, all three species deliver milk at a similar high rate (1.0, 2.1, and 1.3% of female weight per hour in California sea lions, harp seals, and northern elephant seals, respectively).

5.2. The Energetics of Lactation

From data on milk yield and milk energy content, it is possible to estimate both daily milk energy output and the total energy output for lactation (Table XIV). Among terrestrial mammals, peak milk energy output scales to metabolic size ($\text{weight}^{0.75}$), but the level of production is affected by litter size and mass (Oftedal, 1984b). Pinnipeds exhibit great variation in milk energy output per maternal metabolic mass, but this variation appears to be a function of lactation length (Table XIV). As lactation length increases, energy output per unit metabolic size falls from 991 kcal/kg^{0.75} per day in the hooded seal to 181 kcal/kg^{0.75} per day in the Weddell seal and to 85 kcal/kg^{0.75} per day in the California sea lion. A Pearson's correlation analysis on these data, using log transformation, indicates a correlation between energy output and lactation length of 0.976 (d.f. = 4, $P < 0.001$). In this case phocids and otariids form a continuum.

Total output of milk energy follows the reverse trend—as lactation length increases, total energy output per maternal metabolic mass rises (Table XIV). Thus total milk energy output per kg^{0.75} in Weddell seals (8.15 Mcal/kg^{0.75}) is about 2.5 times that of hooded seals (3.31 Mcal/kg^{0.75}). The data for the two otariids represent an extrapolation from the first 60 days to the entirety of lactation and may be substantially in error if either daily milk yield or the energy content of milk changes markedly in the latter part of lactation. In California sea lions both milk yield and milk energy content appear to increase in the fourth month (Tables VIII and XIV), such that the extrapolated value in Table XIV is probably an underestimate. Lactation length was assumed to be 300 days because

TABLE XIV
Estimates of Milk Energy Output in Pinnipeds^a

Species (lactation duration, days)	Daily EO (Mcal)	Daily EO per MMBS (kcal/kg ^{0.75})	EO per pup gain (Mcal/kg)	Total energy output (Mcal)	Total EO per MMBS (Mcal/kg ^{0.75})	References
Hooded seal (4)	48.5	991	8.85	162	3.31	O. T. Oftedal, D. J. Boness, and W. D. Bowen (unpublished)
Harp seal (12)	16.1	408	7.66	193	4.88	O. T. Oftedal, D. J. Boness, and W. D. Bowen (unpublished)
Northern elephant seal (27)	23.0	215	6.95	610	5.69	Costa et al. (1986)
Weddell seal (45)	17.6	181	8.89	792	8.15	Tedman and Green (1986)
Northern fur seal ^b (120)	2.14	141	22.8	260?	17?	Costa and Gentry (1986)
California sea lion ^c (~300)	2.44	85	20.6	730?	25?	O. T. Oftedal, S. J. Iverson, and D. J. Boness (unpublished)

^aBased on milk yields in Tables XII and XIII. EO, Energy output; MMBS, maternal metabolic size (kg^{0.75}).
^bDaily energy output measured 0–60 days; extrapolated to 120 days to obtain rough estimate of total energy output (see text).
^cDaily energy output measured 0–60 days; extrapolated to 300 days to obtain rough estimate of total energy output (see text).

some pups are beginning to feed at this time (D. J. Boness and O. T. Oftedal, unpublished). The estimated total energy yields for the northern fur seal (17 Mcal/kg^{0.75}) and California sea lion (25 Mcal/kg^{0.75}) are about twice and three times, respectively, that of the Weddell seal, suggesting that otariid lactation involves much greater energy outlays than does lactation in phocids.

By comparison, estimated total milk energy output in ungulates ranges from 7 to 13 Mcal/kg^{0.75} (Oftedal, 1985). Thus, Weddell seals fall within the ungulate range, whereas the pack-ice species have much lower and the otariids much higher energy outputs per maternal metabolic mass.

Milk energy output can also be estimated indirectly from data on the storage and expenditure of energy by suckling pups (Fedak and Anderson, 1982; R. E. A. Stewart and Lavigne, 1984). In the absence of direct data on metabolic rates of suckling pups or on the efficiency of energy utilization for growth and metabolism, a number of assumptions and extrapolations have to be made. Nonetheless, estimates of daily milk energy output developed for both harp seals (563 kcal/kg^{0.75} per day; R. E. A. Stewart and Lavigne, 1984) and grey seals (362 kcal/kg^{0.75} per day; Fedak and Anderson, 1982) are similar in magnitude to values obtained from data on milk composition and yield (Table XIV). The correspondence of the two harp seal estimates (563 compared to 408 kcal/kg^{0.75} per day) is improved if lactation length is taken as 12 days (Kovacs, 1986) rather than 9 days (R. E. A. Stewart and Lavigne, 1984); the recalculated value is then 422 kcal/kg^{0.75} per day. R. E. A. Stewart and Lavigne (1984) estimate that total milk energy output over lactation is 194 Mcal in harp seals, an identical value to that estimated from milk yield (Table XIV). Grey seals lactate for 17 days (Table II), during which total milk energy output can be calculated as 289 Mcal (6.1 Mcal/kg^{0.75}; Fedak and Anderson, 1982). This value is only 10–20% higher than would be predicted from the estimates in Table XIV. The relatively good correspondence of estimates obtained by independent methods suggests that the errors of estimation are either small or similar for the two approaches.

6. SUMMARY OF THE LACTATIONAL STRATEGIES OF PINNIPEDS

6.1. Conflict between Foraging and Nursing

Reproductive strategies in pinnipeds are molded by the constraint that birth and early postnatal development must occur on a solid sub-

strate of land or ice. With the exception of the walrus, nursing of pups always occurs on this solid substrate. Nursing and foraging at sea are thus mutually exclusive activities. Although terrestrial carnivores typically hunt prey and nurse their young in separate locations, feeding sites of pinnipeds may be far removed from suitable sites for pup rearing.

The three pinniped families have adopted three diverse strategies in coping with the potential conflict between foraging and nursing—female phocids typically abandon feeding during lactation, female otariids intersperse feeding periods with periods of nursing, whereas female odobenids take their young to sea at an early age and nurse them in the water. The major components of these three strategies will be briefly summarized. Variations among species in the behavioral, physiological, and anatomic aspects of these strategies have been reviewed in the body of this paper.

6.2. The Phocid Strategy: Fasting and Intensive Lactation

The phocid strategy of fasting during lactation requires that virtually all nutrients required for lactation be stored in maternal tissues prior to parturition. In the harp seal most energy accumulation occurs in the few months preceding parturition (W. D. Bowen, personal communication). Because energy and nutrient accumulation precedes lactation, and the lactational fast represents a loss of feeding opportunity, one would expect phocids to time parturition to coincide with the end of a period of seasonal food abundance. The short duration of the pupping season and the prevalence of migration in many phocids (Table II; Section 2.1) is consistent with the hypothesis that seasonality in food resources may be important.

Because the lactating phocid must support both milk production and maintenance metabolism by drawing on body reserves, any reduction in maintenance costs will increase the proportion of reserves that can be devoted to pup rearing. One way to reduce maintenance costs is to shorten the duration of lactation such that fewer days of maintenance metabolism must be supported. Relatively short lactation periods are characteristic of most phocids (Table II); at the extreme, the hooded seal has the shortest lactation of all mammals. Phocid pups are typically weaned abruptly upon female departure from the birth site (Section 2.5), and fast for 1–10 weeks before feeding on their own (Bowen et al., 1986b).

Abbreviation of the lactation period requires that the rate of energy transfer from mother to pup and the resultant rate of pup growth be

accelerated, or the pup may not reach a weaning weight adequate for survival (Bowen et al., 1985; Kovacs and Lavigne, 1986). Indeed, both the relative rate of energy transfer (Section 5.2; Table XIV) and the relative rate of pup growth (Kovacs and Lavigne, 1986) are negatively correlated to duration of lactation in phocids. At the extreme, a hooded seal achieves a daily milk energy output equivalent to the combined peak production of milk energy by four to seven terrestrial carnivore mothers or seven to 15 ungulate mothers (Oftedal, 1984a, 1985). Females of species with longer lactation periods, such as northern elephant and Weddell seals, transfer energy to single pups at a rate equivalent to the peak output of terrestrial carnivores with large litters.

High rates of energy transfer to phocid pups are achieved by secretion of high-fat, high-energy milks (Table VIII) in substantial amounts (Table XII). Because milk lipids appear to derive from body stores with relatively little modification (Section 3.2), the energetic efficiency of fat secretion is undoubtedly high. The secretory mechanisms whereby milk of such high fat and low water content is produced are not understood, especially given the negligible amounts of sugars and unusual potassium-to-sodium ratios that are typical of both phocids and otariids (Tables VIII and XI). High rates of fat secretion may underlie the relatively large size of fat droplets in mammary secretory cells (Fig. 5), and the reduced relative volume of Golgi vacuoles in these cells may reflect low rates of aqueous phase secretion. In other regards, mammary tissue of phocids is comparable in gross anatomy and ultrastructure to other mammals (Sections 4.1–4.3). Limited data suggest that the relative size of phocid mammary glands exceeds the mammalian norm.

Given the rapid rate of energy transfer from mother to pup, one might expect phocid pups to spend more time in suckling activities than terrestrial mammals, but neither suckling frequencies nor suckling durations (Table III) are exceptional by comparison to other mammals. Thus, the high rates of transfer are a function of the high energy density of milk rather than modifications in suckling behavior. Female phocids remain in the vicinity of their pups throughout lactation, but in some species females enter the water and a minimal amount of maternal feeding may occur (Table IV). Water entry may be as much related to thermoregulation, sexual activity, or predator avoidance, however (Section 2.3.4).

6.3. The Otariid Strategy: Alternation of Foraging and Nursing

Nutrient stores of otariid females are apparently adequate to support lactation for about 1 week after birth; thereafter females depart the

rookery on foraging trips of about 1–6 days duration (Table V). Foraging trips are alternated with time at the rookery when pups suckle. One-half to three-quarters of the lactation period of 4–12 months or longer (Table II) is spent at sea on foraging trips (Table V). Otariid pups devote more time to suckling when females are present than do phocid pups, which may help compensate for the briefness of maternal visits (Section 2.3.3).

The necessity of feeding has undoubtedly limited potential pupping sites to those within a reasonable swimming distance of foraging grounds; conversely, during lactation otariid females are unable to rely on pelagic resources at a distance from land. In contrast to phocids, otariids would be expected to time parturition such that seasonal food resources would become locally abundant during lactation, when successful foraging is essential to sustained milk production, pup growth, and pup survival.

The intermittent pattern of milk transfer results in a cycle of feeding and fasting for the otariid pup. Although milk intakes may be quite large when mother is in attendance, average intake calculations reflect the periods of fasting and are thus much lower than for phocid pups (Table XIII). Otariid pups require energy to support metabolic requirements on both fast days and days that milk is consumed. Maintenance requirements of pups are thus quite high and the efficiency of growth is consequently low (Oftedal et al., 1985). Suckling otariid pups ingest 6 kg or more milk/kg weight gain (Table XIII), as compared to 1.5–2.0 kg milk/kg weight gain in phocid pups (Table XII). It is not surprising that otariid pups exhibit slow growth rates and a prolonged period of dependence on maternal milk. Otariid pups are typically weaned at a weight somewhat greater than one-third of maternal weight (Gentry et al., 1986).

In most mammals a prolonged interval between suckling episodes leads to the onset of mammary involution with associated degradative changes in secretory epithelium. The mechanisms whereby female otariids avoid these changes during prolonged foraging bouts remain a mystery (Section 4.5). Incomplete data on mammary dimensions of the northern fur seal suggest that mammary gland volume may be quite large, but milk storage capacity of the mammary system has not been measured. The secretion of high-fat, energy-dense milk by otariids (Table IX) may be one means of minimizing mammary storage requirements during foraging trips, as well as facilitating rapid nutrient transfer to the pup during suckling periods ashore. It is not known whether secretion rates of milk or milk constituents change while the female is at sea or in response to suckling stimuli on land.

Although the average daily rate of milk energy transfer to pups is much lower in otariids than in phocids, the longer duration of lactation in otariids results in greater total energy outlays in milk over the course of lactation in this group (Table XIV). It appears that otariids have adopted a lactation strategy that is energetically expensive, but the costs are spread over time and can therefore be met by ongoing foraging activities.

6.4. The Odobenid Strategy: Aquatic Nursing

An obvious solution to the conflict between rearing pups on a solid substrate while foraging at sea is to evolve a pattern of aquatic rearing of the young. Yet no pinniped routinely gives birth at sea, and the sole extant odobenid, the walrus, is the only species that has evolved a pattern of aquatic suckling. Walrus pups abandon their birth sites on pack ice at an early age and accompany their mothers to sea, suckling both in the water and at haul-out sites (Fay, 1982; Miller and Boness, 1983). Thus, female walrus face neither the constraints on foraging activities and suckling patterns inherent in the otariid strategy of intermittent feeding nor the constraints on lactation duration arising from the phocid approach of fasting.

Unfortunately, relatively little is known about lactation in this unique species. Pups are apparently dependent on milk alone in the first 5 months after birth and then wean gradually to benthic invertebrates, being fully weaned by 2–3 years of age (Fay, 1982). This represents the longest lactation known for any pinniped. A few milk samples from the first month postpartum have been reported to contain moderate but variable amounts of fat (14–32%) and protein (7–11%), similar to early lactation samples in some otariids and phocids (Section 3.1.2). Some data are available on suckling duration on land and in water, but suckling frequency has not been studied (Section 2.3.3). Both mammary structure and function and lactation energetics of the walrus are unknown. Further study is needed to elucidate the consequences of aquatic suckling to the odobenid lactation strategy.

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