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Chapter

Lactation Strategies and Milk Composition in Pinnipeds

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Abstract

Maternal investment during lactation is higher than during gestation, and it is the most energetically expensive period in a mammal's life cycle. Pinnipeds (seals, sea lions, fur seals, and walruses) are one of the principal groups of aquatic mammals that are adapted to reside on land and at sea. During lactation they secrete and rapidly transfer lipid-rich and energy-dense milk to the pup, and they rely on land or ice to give birth to and nurse their pups, and as a consequence, foraging at sea and nursing of the young on land are separated by space and time. Lactation strategies in pinnipeds have evolved to meet particular environmental conditions, and because of their worldwide distribution, they have evolved into two main lactation strategies: fasting strategy and foraging strategy. Both strategies rely on energy reserves for the production of energy-dense and nutrient-rich milk. In comparison with the milk of land and marine mammals, the milk of pinniped is characterized by (a) high milk fat concentration and (b) the virtual absence of lactose. These two main differences in the milk composition are a result of the lactation strategies adopted by pinnipeds and their unique lactation physiology in which they need to transfer a high energy-rich milk in a certain period of time while conserving water.

Keywords: milk, lipid, protein, pinnipeds, pup, seal, sea lion, walrus, foraging, fasting, marine mammals

1. Introduction

Maternal investment during lactation is higher than during gestation, and it is the most energetically expensive period in a mammal's life cycle [1, 2]. In early postnatal life, the neonate is unable to feed itself; hence, it has to rely on the mother for its food supply in the form of milk, and this process of milk production is known as lactation [3]. As a consequence of the full dependence on the female during lactation, parental investment will have a direct effect on the growth rate and survival of the nursing offspring. On the other hand, mammal reproductive success will be influenced by parental age, experience and foraging strategies, and food availability; but also by factor associated to the offspring such as time of weaning, sibling competition, and litter size [4].

Pinnipeds (seals, sea lions, fur seals, and walruses) are one of the principal groups of aquatic mammals that are adapted to reside on land and at sea [5, 6]. There are three taxonomic groups of pinnipeds, Otariidae, the sea lions and fur seals; Odobenidae, the walrus; and Phocidae, the true seals, and they have adopted

distinctive lactation strategies [6, 7]. They rely on land or ice to give birth and nurse their pups, and as a consequence, foraging at sea and nursing of the young on land are separated by space and time [6, 7]. While staying on the terrestrial environment, for some species, the mother and the pup are vulnerable to potential terrestrial predators; therefore, pinnipeds have evolved strategies to diminish the risk of predation [7, 8]. Other issues that concern the survival of the pup are (1) the buildup of an insulation layer against heat loss and (2) the supply of enough energy to enable the pup to sustain itself during periods of fasting. These issues are tackled by secreting and rapidly transferring lipid-rich and energy-dense milk to the pup [9, 10]. Lactation strategies in pinnipeds have evolved to meet particular environmental conditions, and because of their worldwide distribution, they have evolved into a diversity of lactation strategies [7, 8, 11]. In this chapter the lactation strategies of pinnipeds are described; and the milk composition of pinnipeds and how its composition varies in relation to maternal factors are discussed.

2. Lactation strategies in pinnipeds

2.1 Foraging lactation strategy: sea lions and fur seals (Otariidae)

Otariids have adopted a lactation strategy known as the "foraging lactation strategy" or as "income breeders," and it is characterized by the mother alternating between nursing the pup on land and periods of foraging at sea (**Figure 1**) [12]. The perinatal period is known as the time period in which the otariid mother stays on land with the pup after giving birth. During this period, which last about a week, the pup-mother bond is established.

The duration of lactation in otariids ranges from 4 months to 3 years (**Table 1**) [7] and may have evolved as a consequence to environmental predictability associated with latitude [11]. The predictability and productivity of the marine environment have had a crucial role in shaping the maternal strategies observed in pinnipeds. For instance, in higher latitudes marine productivity is seasonal and radical; however, very predictable. The duration of lactation in pinnipeds is usually short in higher latitudes, whereas in lower latitudes, the seasonal pattern of marine productivity is more constant throughout the year, and as a result, the duration of lactation in pinnipeds is usually longer (**Table 1**). Notwithstanding, every few years pinniped inhabiting lower latitudes are exposed to unpredictable productivity due to El Niño/La Niña (El Niño Southern Oscillation or ENSO) conditions, [13]. El Niño Southern Oscillation events have a profound effect on climate and ocean
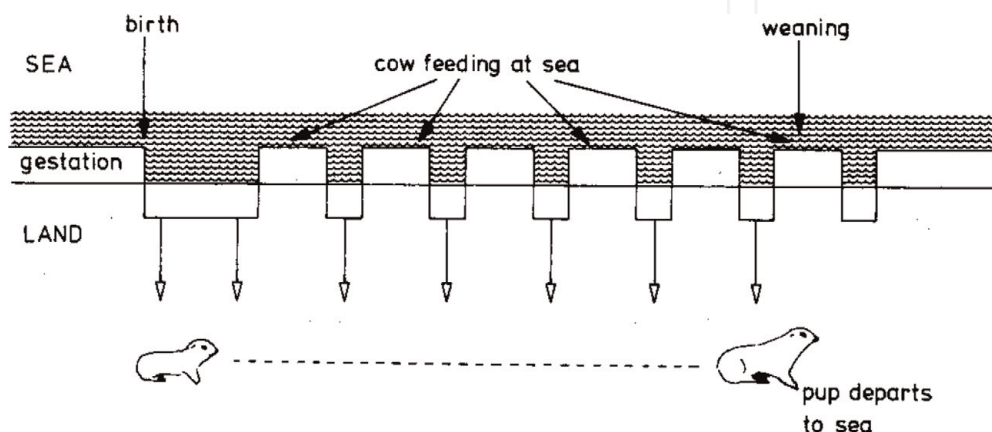

Figure 1.
Maternal foraging strategy of otariid seals (from [7]).

Species	Lactation (months)	Source
Northern fur seal *Callorhinus ursinus*	3–4	[23, 25, 32]
Antarctic fur seal *A. gazella*	4	[4, 26, 32]
South American sea lion *Otaria flavescens*	5–12	[5, 7]
California sea lion *Zalophus c. californianus*	6–12	[17, 19, 33]
South American fur seal *A. australis*	6–24	[7, 16, 34]
Juan Fernandez fur seal *A. philippii*	7–10	[35]
Subantarctic fur seal *A. tropicalis*	10	[9, 36]
Australian fur seal *A. pusillus doriferus*	11	[30]
Guadalupe fur seal *A. townsendii*	9–11	[32]
Steller's sea lion *Eumetopias jubatus*	11–12	[37–39]
New Zealand fur seal *A. forsteri*	11–12	[7, 40, 41]
New Zealand sea lion *Phocarctos hookeri*	~12	[42]
Galapagos sea lion *Zalophus c. wollebaeki*	~12	[5, 21]
Cape fur seal *A. pusillus pusillus*	~12	[7, 43]
Walrus *Odobenus rosmarus*	12–36	[5, 7, 44]
Galapagos fur seal *A. galapagoensis*	12–36	[7, 21, 32]
Australian sea lion *Neophoca cinerea*	15–18	[1, 2]

Table 1.
Duration of lactation period in fur seals, sea lions, and walruses.

ecosystems [14]. Upwelling zones in the eastern Pacific undergo a negative transition from normal highly rich productivity to profoundly decreased productivity [15]. Pinnipeds which prey at the top of the food chain are severely affected by low food availability, which in turn disrupts normal maternal foraging and attendance patterns, suckling patterns, pup growth, and pup behavior [16, 17].

During El Niño conditions, changes in the maternal attendance pattern (nursing behavior) and maternal diving behavior of South American fur seals (*Arctocephalus australis*) have been recorded [18]. Shortage of food availability due to ENSO conditions resulted in low maternal foraging success and prolonged stay at sea searching for food at high-energy cost. Consequently, South American fur seals nursing mothers were unable to replenish their energy reserves to confront the high-energy cost of lactation. California sea lions (*Zalophus californianus*) responded in a similar manner to ENSO conditions by extending significantly their foraging trips [19], and pup milk intake was lower than in years without El Niño conditions [17]. During years of shortage of krill near South Georgia, lactating Antarctic fur seal (*Arctocephalus gazella*) females made fewer and longer trips that resulted in decreased mass and growth of pups [4]. The maternal foraging trips doubled in time, and as a consequence, the mortality of pups increased to 32%, 68% which died from malnutrition [20].

Among otariid species they share very similar breeding and lactation strategies (see **Figure 1**) [7]. In low-latitude otariids, such as Galapagos fur seals, during pregnancy they spend extended periods of foraging at sea in order to store energy in the form of lipid, and then they arrive at the colony 2–3 days before giving birth. Thereafter the mother nurses the pup during the perinatal period (5–10 days), and then she starts her attendance pattern that consists of foraging trips at night and return to the colony in the morning [21]. Foraging trips lasted around 2 days [21], whereas suckling attendance periods lasted from half a day to one and a half days,

the length of which is related to the age of the pup [22]. The tropical Galapagos fur seals have the longest lactation period in otariids that lasts from 1 to 3 years (**Table 1**). Their conspecific, the Galapagos sea lions (*Zalophus californianus wollebaeki*), attended their pups almost every day and foraged during the day and returned at night [21].

In comparison with otariids inhabiting low latitude, species with high-latitude distribution have shorter lactations period (e.g., Antarctic fur seals, northern fur seals *Callorhinus ursinus*, and subantarctic fur seals *Arctocephalus tropicalis* (see **Table 1**)). Antarctic and northern fur seals wean their pups at the age of 4 months, while subantarctic fur seals wean their pups at the age of 10 months (**Table 1**) [5]. Pregnant Antarctic fur seals arrive at the colony 2 days prior parturition, and their perinatal period lasts for about 5–7 days, and then the mother alternates foraging at sea for 3–5 days with attendance periods of 3–10 days [23, 24]. Similarly, pregnant northern fur seals arrive to the colony 12 hours to 2 days prior to the birth and nurse their pup during the 6–7 days perinatal period before commencing their first post-partum foraging trip that could last 4–7 days [23, 25].

The mean duration of foraging trips of lactating northern fur seals lasted for 6–8 days and was longer than in Antarctic fur seals, while their attendance period lasted from 36 hours to 2 and a half days. Interestingly, subantarctic fur seals have one of the longest attendance pattern recorded in fur seals. The females arrive ashore 1–2 days prepartum and then spend 8 days nursing the newborn, thereafter alternating long foraging trips of 11–23 days with long maternal attendance periods ashore of up to 4 days [26, 27]. This attendance pattern is constant throughout the whole period of lactation and until the pup is weaned at 10 months of age (**Table 1**) [26].

In conclusion, otariids inhabiting low latitudes are exposed to a marine environment with very unpredictable low food productivity, while otariid mothers raising their pups at high latitudes have to deal with a more predictable marine environment with high seasonal productivity.

Given the degree of the predictability of the food productivity in the marine environment, one may expect to observe shorter lactation duration in subpolar otariid species due to the short high-productivity seasonal period. However, some species data contradict this argument and cannot be sustained.

Therefore, it could be argued that the duration of lactation in otariids might be a result of the seasonal availability and predictability of food sources, while foraging trip duration and rate of energy transfer are determined by the distance from the breeding site ashore to the food source at sea [6]. Some investigators have raised the question whether milk composition in otariids is directly or indirectly influenced by interspecific differences in the duration of foraging trips at sea [9, 10, 21, 28–31].

2.2 Fasting lactation strategy: *seals* (Phocidae)

Phocid maternal strategies differ from that of the otariids, mainly by a shorter lactation period and maternal fasting throughout the whole lactation period (**Figure 2** and **Table 2**). Phocids have adopted a lactation strategy known as the fasting lactation strategy making them capital breeders [12]; however, not all phocid species are embedded into this strategy. Pregnant phocid females arrive at haul-out sites a few days before pupping, and when nursing is completed, the pup is abruptly weaned (**Figure 2**) [5]. Phocid seals that breed on pack or fast ice are known as pagophilic seals, while seals that breed on dry land are known as land-whelping seals [7].

Ice-breeding seals or pagophilic seals (breed on pack or fast ice) [7] have evolved remarkable breeding and lactation strategies in order to reduce predation pressure.
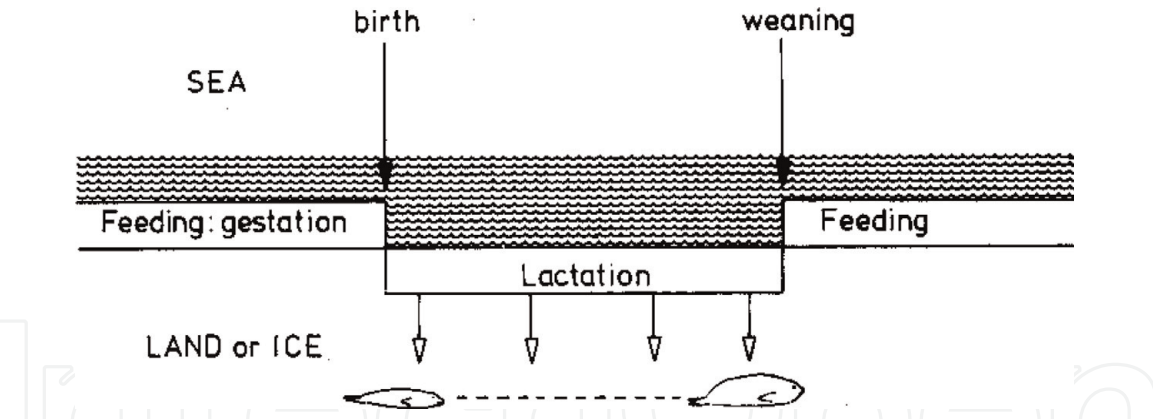
Figure 2.
Diagram of the breeding and lactation strategy of true seals, phocids, known also as the fasting strategy, and capital breeders [7].

Species	Lactation period (days)	Source
Pack ice		
Hooded seal *Cystophora cristata*	4	[48]
Harp seal *Phoca groenlandica*	12–13	[49]
Crabeater seal *Lobodon carcinophagus*	14–21	[50]
Bearded seal *Erignathus barbatus*	12–24	[51]
Gray seal *Halichoerus grypus*	16	[5]
Caspian seal *Phoca caspica*	21	[52]
Ribbon seal *Phoca fasciata*	21–28	[53]
Spotted seal *Phoca largha*	28	[5, 54]
Leopard seal *Hydrurga leptonyx*	∼30	[55]
Fast ice		
Weddell seal *Leptonychotes weddellii*	35–42	[56]
Ringed seal *Phoca hispida*	36–41	[57]
Baikal seal *Phoca sibirica*	60–75	[58]
Land		
Harbor seal *P. v. richardsi*	21–35	[52]
Southern elephant seal *Mirounga leonine*	23	[59, 60]
Northern elephant seal *M. angustirostris*	28	[61, 62]
Harbor seal *Phoca vitulina vitulina*	28–42	[63]
Harbor seal *P. v. concolor*	33	[52]
Hawaiian monk seal *Monachus schauinslandi*	∼42	[64, 65]
Mediterranean monk seal *M. monachus*	42–49	[65, 66]
Harbor seal *P. v. Stejnegeri*	90	[52]

Table 2.
Duration of lactation (days) in true seals (phocids) breeding on three different substrates: pack-ice, fast-ice, and land.

In order to do so, phocids have shortened the duration of lactation, and they have inhabited higher-latitude breeding substrate in which terrestrial predator area is almost nonexistent [7]. However, fast-ice phocids such as ringed seals

(*Phoca hispida*) are preyed by polar bear and arctic fox and have avoided predation pressure by giving birth and nursing their pups in snow and ice dens [45, 46]. If predation is nonexistent or basically avoided by choice of breeding site, then any variations in the maternal strategies must be related to other ecological factors such as stability of breeding substrate.

There are some advantages and disadvantages for phocid breeding on ice packs (ice floating on the sea surface). Seals have a rapid access to deep waters; however, ice packs provide little shelter and are an unstable substrate at the mercy of wind and sea surface currents that could drift away the ice pack separating the mother and pup. As a consequence of the instability of the pack-ice breeding, pagophilic seals have the shortest lactation period in pinnipeds (4–30 days) [5, 7, 47]. On the contrary, in more stable environments such fast-ice or land, seals are able to extend the duration of the lactation period (36–75 days).

The shortest lactation period in pack-ice-breeding species has been reported in the hooded seal, *Cystophora cristata*, that nurses pups for only 4 days [47], and the harp seal, *Phoca groenlandica*, for 12–13 days [67], while the longest lactation period has been recorded in seals that breed on fast-ice and land (**Table 2**). In comparison with the duration of lactation in Baikal seals and the Mediterranean monk seals, southern (*Mirounga leonina*) and northern elephant seals (*Mirounga angustirostris*) have significantly shorter periods of 21 and 28 days, respectively (**Table 2**). The short lactation duration described in phocid in comparison with otariids and maternal fast during the nursing period influence the milk composition and the dynamics of energy transfer from mother to pup. Moreover, the high milk energy content in phocid could be a result of the short lactation duration in which a large amount of energy in the form of milk lipid and protein is transferred to the nursing pup in a limited time.

Two distinctive lactation strategies have been observed in ice-breeding seals (e.g., hooded seals and gray seals, *Halichoerus grypus*). In the first lactation strategies, seal mothers nurse their pup with very energy-rich milk during a very short lactation period (**Tables 2** and **3**). This lactation strategy involves the pup being very inactive and in most cases does not enter the water for many weeks, and they are abruptly weaned, and then the pup must withstand a long postweaning fasting period [68].

The second lactation strategy is observed in bearded seals *Erignathus barbatus* and ringed seals *Phoca hispida* and has the longest lactation duration among ice-breeding phocids. In addition, nursing mothers do not fast entirely during the lactation period, the energy content in milk is lower, and pups are more active. It was argued that only otariids have evolved a foraging lactation strategy in which lactating females have pup attendance periods on land alternated with foraging trips at sea.

Research about the energetics and diving behavior of harbor seals (*Phoca vitulina*) has demonstrated that maternal body mass has important consequences for lactation strategies in phocid species and that some phocids have adopted an "otariid like-lactation strategy" [69]. This may in fact suggest that ice-breeding seals such as bearded and ringed seals, with long lactation duration and lower energy-rich milk, are unable to sustain lactation while fasting. There is data that support the hypothesis that these seals have adopted an "otariid-like" maternal foraging cycle [57, 70, 71]. An otariid-like foraging cycle behavior may have evolved in small body size phocids, such as the harbor seal, as a result of depletion of maternal body energy reserves in the form of lipid during the lactation period [6]. The maternal body size of harbor seals is slightly larger than most otariids, suggesting that the body size may be limiting the amount of energy reserves (lipid)

Species	Milk composition (%)				
	Lipid	Water	Protein	Sugar	Ash
Australian sea lion[+] [2, 28]	28.35[a]	56.9 ± 9.9	9.9 ± 2.5	—	0.9 ± 0.3
	47.15[b]	—	—	—	—
	55.4[c]	—	—	—	—
Steller sea lion [37]	24	—	—	—	—
South American sea lion [81]	38.6 ± 3.1[a]	48.9 ± 3.1	11.1 ± 1.2	—	0.8 ± 0.1
California sea lion [17]	31.7[a]	59.0	8.5	0.3	—
	43.7[b]	—	—	—	—
Galapagos sea lion [21]	32.4[a]	—	9	—	—
	25.1[b]	—	—	—	—
New Zealand sea lions [82]	21.3 ± 8.1	67.9 ± 8.8	9.4 ± 2.4	0.4	0.48 ± 0.06
Galapagos fur seal [21, 83]	29.4 ± 5.9[a]	—	9.9 ± 1.4[a]	0.1	0.9 ± 0.1
	—	—	14.0 ± 0.9[b]	—	—
Guadalupe fur seal [10]	∼41	—	—	—	—
Juan Fernandez fur seal [29]	41.4 ± 5.8	—	11.9 ± 2.0	1.2 ± 0.4	0.7 ± 0.1
Subantarctic fur seal [10]	45.0 ± 3.7[a]	40.7 ± 4.5[a]	13.4 ± 1.4[a]	—	—
	51.9 ± 4.9[b]	33.3 ± 4.0[b]	11.6 ± 1.3[b]	—	—
	52.3 ± 6.0[c]	33.3 ± 4.9[c]	11.5 ± 1.2[c]	—	—
South American fur seal [84]	36.5 ± 4.2	—	9.1 ± 0.8	—	—
Australian fur seal[*] [30]	32.7[a]	54.6[a]	9.9[a]	—	0.7 ± 0.1
	47.7[b]	39.1[b]	11.0[b]	—	—
	47.9[c]	44.3[c]	12.3[c]	—	—
Cape fur seal [85]	23.2[a] ± 8.2	58.1 ± 6.8	10.8 ± 1.2	—	2.0 ± 0.6
Northern fur seal [7, 86]	45.6	36.4	12.4	0.1	0.6
Antarctic fur seal [3, 9]	39.8 ± 6.7	41.3 ± 9.3	18.1 ± 5.8	—	0.7 ± 0.1
Walrus [79]	24.1	59.9	7.8	—	0.59

[a]*Early lactation*
[b]*Mid lactation*
[c]*Late lactation*
[*]*Values estimated from regression equations (see Arnould and Hindell) [30]*
[+]*Values were averaged.*

Table 3.
Milk composition of otariids and walrus.

that can be stored. The demand of energy from her limited body's stored reserves (blubber) to produce milk and to maintain her own energy needs may not be enough [6, 72–74].

Taken into consideration the small maternal body size of harbor seals, it is very likely that at least half of the phocid species with similar small body size may have adopted the "otariid-like" maternal foraging cycle [73]. There is evidence that shows that lactating harbor seal started to forage at sea when the gain of energy, to restore energy reserves, was highest and the uncertainty of pup mortality was the lowest [73]. Maternal body size has been shown to play an important role in shaping lactation strategies in pinnipeds [8]. For instance small body size phocids, cannot store enough energy in the form of blubber (lipid) to support the high cost of lactation, and thus, there are physiological limits that are interacting and influencing their lactation strategy [6, 69].

Northern and southern elephant seals have a similar breeding pattern, and a wide variety of social behavior traits (age, sex, and season) are a result of well-defined seasonal cycles and making of large colonies. Within the group of land-whelping seals, elephant seals have one of the shortest lactation periods, lasting 23 days in southern elephant seals and 28 days in northern elephant seals. During this period the pup has a rapid growth rate [59, 75], and it is followed by a long postweaning fasting period (2–3 months) [76]. Notwithstanding during this period, male pup steals milk from other mothers in order to grow bigger, and this is driven by a marked sexual dimorphism in elephant seals, i.e., there is a selective advantage in increased size in males (**Figure 3**).

A mentioned before, small maternal body size phocids species have adopted alternative "otariid-like" lactation strategies within their group. In this context it may be possible to raise the question what are the factor/s or selective pressure that are governing the maternal strategies in phocids and are they the same as in otariids.

The influence of latitude on the lactation strategies, as described in otariids, have not been suggested for phocids. However, there are environmental factors associated with latitude that may have influenced the evolution of lactation strategies in phocids [11]. The duration of lactation in phocids has evolved, driven by the selective pressure of the breeding substrate and the cost of milk production, and to some extent predation [11]. However, the argument about predation pressure may not apply for most land-breeding phocids since they breed on predator-free islands. Consequently, there must be other selective pressures, apart from the breeding substrate, that caused the shortening of the lactation duration in phocids [11].

In conclusion, the lactation strategy adopted by most phocids is quite unique. Their lactation period is very short in comparison with otariids, and they fast for the entire lactation. As a result they need to store enough energy in body reserves (blubber) in order to produce the most nutrient-rich, energy-dense milk among mammal species. Due to phocid large maternal body size, they store large amount of energy and can withstand the high cost of lactation while fasting. However, small body size phocids such as harbor seals are unable to withstand the cost of lactation due to body nutrient depletion and have adopted an "otariid-like" lactation strategy in which the mother forages at sea.
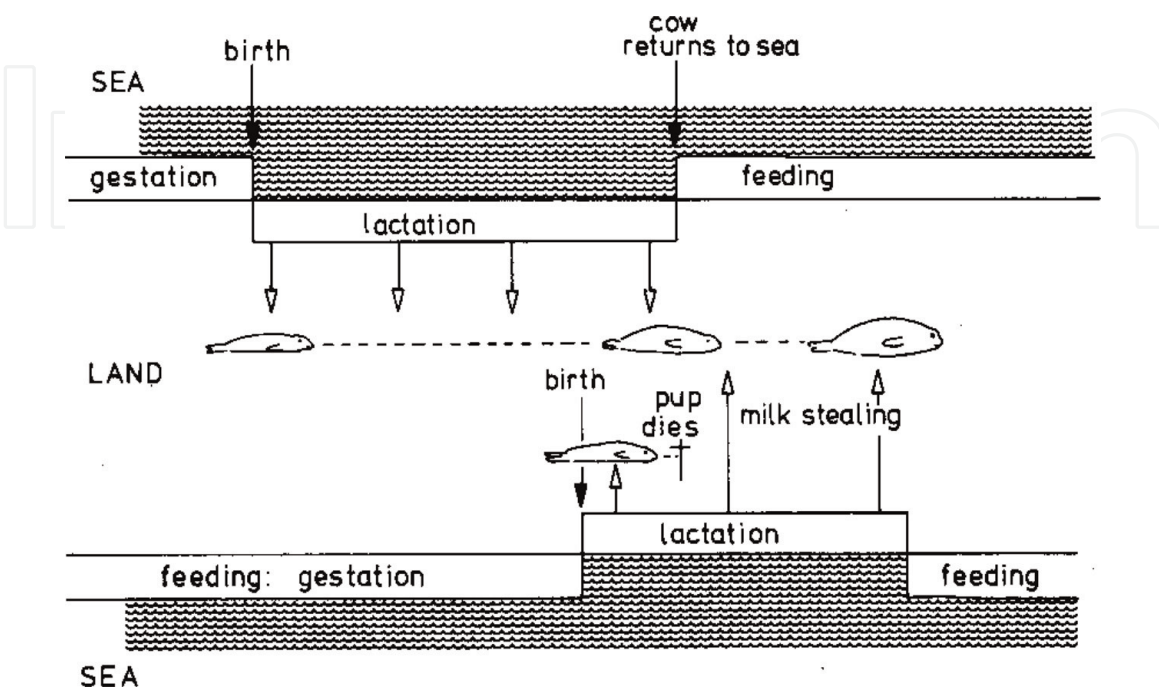

Figure 3.
Fasting lactation strategy in phocids, the northern elephant seals Mirounga angustirostris [7].

2.3 Aquatic lactation strategy: Odobenidae (walrus)

Recapitulating, a third lactation strategy, known as aquatic strategy, has been described in pinnipeds that differ from that of the capital (phocids) and income breeders (otariids). In the northern hemisphere, in high latitudes, two subspecies of walruses occur, namely, the Atlantic walrus, *Odobenus rosmarus rosmarus*, and the Pacific walrus *O. r. divergens* [77]. Walruses are most social among pinnipeds species, and they are usually found in a group on ice floes hauling out, resting, molting, and whelping [78]. In fact, the migration pattern of mother pups pairs is associated with ice movement [79]. At some point in their reproductive cycle, all pinniped species need to return to land or ice to give birth and nurse their pup, and eventually the mother and the pup venture into the sea to search for food. However, walruses have adopted an aquatic lactation strategy in which the mother gives birth to the pup on ice floes, and after the perinatal period (few days), the mother returns to the sea with the pup. Nursing of the pup occurs in the water and on land and ice, and when the mother dives to search for food, the pup remains at the surface [44].

The lactation period lasts for 2 years, and at the age of 5 months, the pup starts to consume solid food, mainly benthic invertebrates [80]. Fisher and Stewart [80] suggested that the long duration of lactation might be associated with the specific mode of feeding of walruses. The main prey of walruses are bivalves (benthic fauna) that inhabit the bottom of the sea [80]. In early stages of lactation, the pup must learn how to dive and search for food at the bottom of the sea, and this may explain the extended duration of lactation that apparently should increase the weaned mass and the survival chances of the pup [44].

Species	Milk composition (%)				
	Lipid	Water	Protein	Sugar	Ash
Harp seal [93–96]	35.8 ± 1.8[a]	51.4 ± 1.8[a]	10.4 ± 0.5[a]	0.69–0.79[a]	0.61
	35.4[b]	32.4 ± 0.4[c]	7.7 ± 0.2[c]	0.65[c]	—
	57.1 ± 0.5[c]	—	—	—	—
Hooded seal [7, 97]	56.3[a]	49.8	6.2[a]	0.86[a]	0.86
	61.0[b]	—	4.7[b]	1.05[b]	—
	61.1[c]	—	5.1[c]	0.99[c]	—
Gray seal [51, 98]	39.8 ± 2.8[a]	45.0 ± 2.1[a]	11.2 ± 0.8[a]	0.7[a]	0.69
	55.6 ± 1.6[b]	3.0 ± 1.4[b]	9.4 ± 0.14[b,c]	0.8[b,c]	—
	60.0 ± 1.86[c]	28.6 ± 1.3[c]	—	—	—
Bearded seal [7, 97]	49.5	46.4	6.8	0.05	0.6
Weddell seal [99, 100]	53.6[a]	43.6	14.1	0.02	—
Harbor seal [6]	50	—	—	—	—
Southern elephant seal [59, 101]	16.1 ± 7.0[a]	70[a]	12.6 ± 2.3[a]	0.28 ± 0.10	—
	39.5 ± 15.2[b]	33[c]	10.7 ± 2.8[c]	—	—
Northern elephant seal [61]	24[a]	75a	5–12	<0.25	—
	47[b]	35[c]	—	—	—
	54[c]	—	—	—	—
Crabeater seal [102, 103]	35[a]	—	10[a]	1.1–1.9	1.04[a]
	50[b]	—	10.8	—	0.93[b]

[a]Early lactation
[b]Mid lactation
[c]Late lactation

Table 4.
Milk composition in true seal, phocids.

In comparison with the milk of pinniped species, the milk produced by walruses contains the lowest lipid and protein concentration (**Table 4**). The low-energy content of milk may be explained by the very long duration of lactation, and hence, there is less pressure in terms of maternal energy reserve depletion and for rapid transfer of energy-rich milk to the pup. Walruses inhabit the same marine environment as pagophilic phocid seals and thus must face the same high thermoregulatory needs and predation pressure. Walruses have evolved an aquatic lactation strategy in which foraging at sea and nursing their pup are not spatially and temporally separated. As a consequence they are able to extend their lactation period, lower the maternal cost (nutrient depletion), and lower pup mortality.

3. Milk composition in pinnipeds and other mammals

Milk is secreted by the mammary glands, and it is a complex fluid that contains five main components, water, lipids, proteins, sugars, and minerals [87–89]. Several of these can be divided further into more specific components. The concentrations of all the components in milk may vary both between species and within species at different stages of lactation and under different nutritional and environmental condition. Extensive reviews of the comparative composition of milk across species can be found elsewhere [87, 90–92]. The milk of pinnipeds differs substantially from other mammals in (a) high-fat concentration in milk and (b) virtual absence of lactose. These differences are a consequence of their lactation strategies and physiology in which the rapid transfer of energy-rich milk and the conservation of water are essential.

Pinnipeds are a group of mammals that produce the richest energy-dense milk, and fat is the major contributor to the energy content of milk. Milk fat concentration varies considerably between pinnipeds species and within species (see **Tables 3** and **4**). Overall phocids produce milk with a higher concentration of fat than otariids although some otariids produce milk with high-fat concentrations (**Tables 3** and **4**). In most species the milk fat concentration varies in response to suckling, and as the mammary gland is being emptied, pinnipeds are not an exception. As in other mammals, milk fat concentration is influenced by stage of lactation and by nutritional status [88]; however, it is not clear how the latter is mediated in pinnipeds. This and other factors that affect milk composition in pinnipeds and in particular milk fat concentration are discussed further (see subsection factors that influence the milk composition) in this chapter.

Milk proteins are either caseins or whey proteins, and the kind and number of protein varies significantly between mammal species [104]. Proteins that are most common in milk are caseins, blood serum albumin, immunoglobulins, and alpha-lactalbumin, and the beta-lactoglobulin family is only found in the milk of ruminants and some species of artiodactyls [104].

Protein such as casein has a nutritional function and is a source of amino acids for the suckling offspring. There is some knowledge about milk proteins and their function in terrestrial mammal; therefore, little can be suggested for homologous proteins found in the milk of pinniped. A whey protein, such as alpha-lactalbumin, has not been found in otariid milk and is practically absent in phocid milk [84, 105, 106]. The protein alpha-lactalbumin is crucial for biosynthesis of lactose in milk, and therefore, the absence of lactose in pinniped milk has been associated with the lack of this protein [86]. By comparison with bovine milk, casein micelles found in northern fur seals milk were significantly larger, but the reason for this has not been addressed [86]. Caseins have been reported to account for 44–72% of the

total protein in phocid milk [87, 107], whereas in otariids, such as northern fur seals and Galapagos fur seals, casein accounted for 52 and 75%, respectively [83, 86, 108].

Moreover, pinniped milk has slightly higher amino acid concentration than in the milk of terrestrial mammal. However, both pinniped mammal species have similar range values for the proportion of total essential amino acids, total branched-chain amino acids, total sulfur amino acids, and most individual amino acids in relation to the total amino acids [83, 109]. Furthermore, the amino acid pattern and total amino acid concentration of milk were affected by stage of lactation in terrestrial mammals but not in pinnipeds [83, 109, 110]. This is contrary to Davis et al. [110] study that suggested that changes in amino acid pattern and total amino acid concentration during lactation were unrelated to phylogenetic order.

There are a great variety of saccharides in milk [111, 112]; however, lactose (disaccharide) is the dominant sugar, and it is synthesized in the mammary gland.

Notwithstanding, the milk of marine mammals contains only traces or no lactose at all. For instance, in human milk more than 100 oligosaccharides or saccharides that contain three or more monosaccharide residues have been observed. The chemical structures of around 80 have been reported [113]. In comparison with measurements of the concentrations of milk fat and protein, carbohydrates have been given little attention in pinnipeds, but data have been reported for Australian fur seals and hooded seal [114], harp seal [106], crabeater seal (*Lobodon carcinophagus*) [102, 115], and Arctic harbor seal (*Phoca vitulina vitulina*) [116]. It has been reported that phocid milk contains several oligossacharides of unknown structure, low concentrations of free lactose, and traces of glucose and galactose [102, 114, 115]. In the milk of most mammals apart from pinnipeds and cetaceans, lactose is the predominant component of carbohydrates [117]. As a consequence, pinnipeds have among the lowest milk carbohydrate concentration of any mammal. The chemical characterization of carbohydrates in hooded seal, crabeater seal and Australian fur seals, California sea lions, and northern fur seals has revealed that, unlike phocids, otariid milk does not contain free reducing saccharides or lactose [86, 102, 105, 106, 114, 118]. The biological function of milk oligosaccharides in phocids may be similar to that in terrestrial mammals, but this does not apply to otariids since they produce milk without free saccharides [114]. The concentration of carbohydrates in Antarctic fur seal milk decreases significantly throughout lactation [3], and similar data on the specific carbohydrates concentrations during the lactation period in otariids species is not available.

Lactose is a carbohydrate usually present in the milk of mammals but is lacking or virtually absent in pinniped milk. The protein α-lactalbumin is an essential component of the lactose synthetase complex, and it is not present in otariid. However, low activity of the protein α-lactalbumin in the milk of northern fur seals have been reported [119] which suggests an altered α-lactalbumin molecule with low biological activity rather than its complete absence in the milk of otariids [120]. The absence of lactose in otariids milk and the presence of traces of lactose in phocids milk are consequences for the need of water conservation [84] and consequently associated to the evolutionary history of pinniped. The need for water conservation is directly related to the secretion of lactose into milk. The later causes movement of water to maintain isotonicity with other body fluids [121] and consequently loss of water.

Furthermore, the virtual absence of lactose in milk could be associated to the inability of otariid to digest this carbohydrate. Most mammalian species are able to digest lactose through intestinal lactase activity, but some pinniped species' intestinal disaccharidases appear to be low [120, 122, 123]. For instance, lactose intolerance in California sea lions pups and adults has been demonstrated [124]; however,

Species	Minerals in milk (mg/kg)													
	Ca	P	Na	K	Mg	Fe	Zn	Cl	Al	Cu	Ba	Cr	Mn	Cd
Harp seal *Phoca groenlandica* [95]	950	708	699	456	104	53	3.6		3.6	1.8	1.8	0.6	0.6	0.1
Giant panda *Ailuropoda melanoleuca* [125]	1.3		0.8	1.7	0.2									
Southern elephant seal *Mirounga leonina* [84]			990	1360										
Northern elephant seal *M. angustirostris* [61]			770	720										
Northern fur seal *Callorhinus ursinus* [86]	567	1193	521	838	141	3.5	9.0	1191		3.7				
Juan Fernandez fur seal *A. Philippii* [126]	731	872												
Galapagos fur seal *A. galapagoensis* [21]	630			1670										
California sea lion *Zalophus californianus* [5]	885	1003	1060	2030										
Polar bear *Ursus maritimus* [127]	290	230												
Black bear *Ursus americanus* [127]	410	280												
Sea otter *Enhydra lutris* [128]	1060	1250												
Spinner dolphin *Stenella longirostris* [129]		1070						455						
Pantropical spotted dolphin *S. attenuata* [129]		1250						468						
Blue whale *Balaenoptera musculus* [130]	310	210	80	130	20			110						
Pygmy sperm whale *Kogia breviceps* [131]	1500	1700												
Weddell seal *Leptonychotes weddellii* [5]			530	570										
Donkey *Equus asinus* [132]	1200	700												
Horse *E. caballus* [132]	800	500												
Common zebra *E. burchelli* [132]	800	500												
Cow [87]	1250	960	580	1380	120			1030						
Human [87]	330	150	150	550	40			430						

Table 5.
Mineral constituents of milk of different species with emphasis on marine mammals.

intestinal lactase activity has been shown in crabeater seal pups [122]. Furthermore, it is also possible that the primary lack of sugar in the milk of pinniped resulted in the loss of the ability to digest lactose. The identification of specific carbohydrates in milk and the role of carbohydrate in milk secretion and as source of energy in pinniped warrant further investigation [3, 86, 114, 118, 121].

Minerals are important component in milk and are present in a variety of chemical forms (see **Table 5**). The major cations in milk are sodium (Na), potassium (K), calcium (Ca), and magnesium (Mg), while the major anions are phosphorus (P) as phosphate, chloride (Cl), and citrate [87, 121]. For instance, there are differences between the ratio Ca/P in pinniped milk (0.5–0.9:1) and terrestrial mammals (1.6:1), and the reason for the inverse Ca/P is unknown [121] (**Table 5**). Na^+, K^+, and Cl^- are the main ions in the aqueous phase of milk of terrestrial mammals, and they play a crucial role in determining milk volume [121]. The amount of lactose secreted determines the volume of milk secreted, and this mechanism maintains the concentration of the ions relatively constant. These solutes act to maintain the isosmotic conditions (same osmotic pressure) between milk and blood by drawing water into the alveolar lumina [121]. Given that lactose is virtually absent in pinniped milk, it is unclear how pinniped controls the secretion of the aqueous phase while maintaining water conservation.

It is likely that in the absence of lactose, the control secretion of the aqueous phase is associated with the higher concentration of Na^+, K^+, and Cl^- and the ratio of Na^+/K^+ (1:1) in pinnipeds in comparison with mammals (Na^+/K^+ is 1:3) [121].

The mechanism controlling the secretion of water in pinnipeds is quite different from that in terrestrial mammals and that further investigation in this area is warranted.

4. Factors that influence the milk composition in pinnipeds

Lactation strategies and milk composition are such important aspects of the reproduction in pinnipeds that they have been the subject of several investigations [5–7, 133–135]. The milk composition of the majority of the pinnipeds species has been described (see **Tables 3** and **4**). Great attention has been given to the factors (stage of lactation, attendance pattern, or maternal body condition) that affect the milk composition in phocid [61, 94, 97, 98]; however, in otariids it is unclear how these factors are influencing its composition. There are methodological issues in the data collection of milk samples that bias the results of the composition analysis and make our understanding of the lactation strategies in mammals difficult. Description of the milk composition of several mammalian species is available [90–92]; however, little attention was given in these earlier reviews to critically evaluate the information presented [117]. The data in the literature on milk composition of pinnipeds are often difficult to evaluate and must be interpreted with caution [99, 117, 136]. Unfortunately, most of these studies are biased due to a few number of samples collected, poor sampling regime, incorrect analytical procedures, and methodological difficulties which consequently make interspecific comparisons difficult [117].

4.1 Milk composition and maternal characteristics

As mentioned before, during lactation, otariid mothers fast during the attendance period on land and then replenish their energy reserves by foraging at sea. In order to fast during lactation, a period of high-energy demand, there must be significant metabolic adjustments such as reduction of glucose use to lower the catabolism of amino acids and tissue proteins for other vital body functions [5].

The milk produced by otariids is low in carbohydrates concentration; therefore lipid and protein make the primary and secondary source of energy in milk (**Table 4**). Without doubt, good maternal body condition at the start of lactation will promote pup growth, and sufficient food intake to replenish energy reserves throughout lactation will enhance reproductive success of the mother [137]. Availability of food and maternal foraging success may be playing an important role in transferring energy to the pup while fasting and even regaining energy while foraging [138]. Consequently it is important to understand the relative contributions of maternal body mass, body condition, age, and foraging success to changes in milk composition and yield in lactating otariids.

Body condition indexes have been widely used in pinnipeds for many reasons: as indicators of nutritional state, to measure the response to environmental perturbations, during molting stage, to relate to reproductive success and growth [20, 48, 82, 139–143]. Two methods of estimating body condition have been used in pinnipeds; one method divides the body mass by body length [139], while the second method estimates the individual residual value of the linear regression between the body mass and body length [141]. Although these methods of body index calculation have not been standardized, making interspecies comparisons difficult, the second method has shown to be a better predictor of the body condition in otariids [82, 144–148].

In South American fur seals in the Pacific Ocean, drastic environmental perturbations such as ENSO changed the attendance and foraging patterns in the lactating females and their foraging success [149]. The low availability of food sources during ENSO resulted in longer maternal foraging trips which may have affected milk quality and volume. Not being able to replenish their body reserves may have decreased their body weight and thus body condition and reduced the benefit to foraging cost ratio [149]. Furthermore, failure in reproductive performance has been also reported in pinnipeds due to changes in body condition. Body condition in Cape fur seal (*Arctocephalus pusillus pusillus*) females influenced their ability to become pregnant or maintain pregnancy [141]. Furthermore, females with poor body condition were less likely to be pregnant than females with better body condition during pregnancy. Also, poor body condition in pregnant Steller's sea lion due to nutritional stress caused lower pup production in the subsequent season [143]. This indicates that food resources were not sufficient to support the energy demands of the reproductive strategy in this species. Similarly, when food resources were scarce for Cape fur seals resulting in low body condition, pregnancy was likely to fail through abortion [141]. In Antarctic waters, variation in food availability in any year has also been associated with low pup production in the following year for Antarctic fur seals around South Georgia [150].

On the other hand, in years when food sources are plentiful, pup production increased and also pup growth, and mothers were able to replenish and store energy body reserves to improve their body conditions for the following breeding season [4, 27]. An increased number of pups were most likely the result of an increase in the number of females in which embryos were implanted and which carried a fetus to term [150]. Lactating otariid females with low foraging success may spend more time at sea and therefore increase the chances of pup mortality due to malnutrition, hypothermia, trauma, or infection and therefore reduce their reproductive success [151, 152].

Given that in other species variation in milk composition indicates the effects of environmental and physiological factors [99, 153, 154], the relationships between these factors and their influence on milk composition in pinnipeds should be investigated. Body mass and body condition are directly linked to individual foraging success and can be used as proxy for the availability of local food resources. Milk fat

has been shown to be correlated with maternal body mass in New Zealand sea lions [82] and Australian and Antarctic fur seals [3, 30], whereas no relationship was found in Australian sea lions [2, 28]. However, body mass is to some degree determined by body length and may not reflect the quantity of body reserves [141], and therefore, body mass may not be a good predictor of the quality of milk. To support this argument, terrestrial mammals such as dog [155] and dairy cows do vary in size within their species but their milk composition does not [156, 157]. Therefore, the variability in milk fat concentration in pinnipeds may have physiological basis rather than influenced by body size [158].

In mammals such as humans and dairy animals (cow and goat), body condition (e.g., cow body condition is scored) determined concentration of fat in milk [159–161]. Similarly, lactating subantarctic fur seals (body mass/body length) and lactating New Zealand sea lions (body condition index) in good body condition produced milk with a greater concentration of lipid [10, 82]. Furthermore, the relationship between BCI and lipid and energy content of milk has been reported for in Australian fur seals and subantarctic fur seals [10, 30]. It appears that individual foraging success may influence body condition and eventually the milk quality in these species.

While the mother is on land fasting and nursing the pup, the milk is initially synthesized from the nutrients that are obtained from the most recent digested food but as nutrient from the intestine is reduced, the nutrients from maternal body stores are mobilized [158]. If this is the case, then females with better body condition (measured from the relationship between body mass and body length) would secrete milk with higher concentration of fat than females with lower body condition. This has been shown in subantarctic fur seals and New Zealand sea lions [10, 82] but remains to be studied in other otariid species.

Female age could be associated with better foraging and reproductive success as older females may have more experience in finding food in years of poor food availability. In addition, full-grown mature females do not need to divert nutrient toward their own growth and thus can divert more nutrient to provide for their pup. Older Antarctic fur seal and northern fur seal females had better reproductive performance than younger females, and this was suggested by greater natality rates, heavier natal pups weights, giving birth earlier in the season, and better possibilities of giving birth the following season [162, 163]. Moreover, in New Zealand sea lion maternal age had a positive effect on the quality of milk, and this could also be attributed to better body condition of older females with more maternal foraging experience than younger females [82]. In Antarctic fur seals, there was no apparent effect of maternal age on the time budget for foraging attendance [164]; however, in years of poor food resources, the foraging time budget was adjusted [24] which increased the cost of foraging in that year by 30–50% [165]. This is consistent with the hypothesis that mothers adjust their behavior to maximize energy delivery to the pup.

Body length has been used as an indirect measurement of age [142, 146, 163, 166, 167]. Maternal age estimated from body length did not increase the concentration of fat in the milk of subantarctic fur seals [10]; however, it did in Australian sea lions [28] and Australian fur seals [30]. Estimating age from body length suffers from bias and is not reliable to assign a pinniped to a particular age [146, 166–169], because the body grows at a progressively decelerating rate with age and the changes within age class and the overlap between age classes are substantial.

Notwithstanding, maternal age may affect and determine their body condition. For instance, young primiparous lactating otariids must be able to store energy reserves and replenish energy at a sufficient rate, in order to withstand the cost of

lactation and her metabolic needs and growth. The mechanisms in which maternal body condition affect the composition of milk in otariids are still unclear. Interannual variability in food sources has direct impact on maternal foraging success and consequently on body condition and thus the female's reproductive success and lactation performance. Some studies have investigated the effect of maternal age on milk composition. Maternal age may influence indirectly the milk composition via body condition, and this hypothesis may be tested in a species for which there are age data.

4.2 Milk composition and attendance pattern

The differences in milk composition among otariid species could be explained by the duration of the foraging trip, i.e., females of a species that make long foraging trip may secrete milk with higher-lipid concentration than a species making shorter foraging trips [21, 31]. In other words, the energy content of milk increases with the length of the foraging trip [135]. This in agreement with the central place foraging theory that postulates that parents that have to make long foraging trip, away from the central place (nest or breeding site), to their feeding grounds should make fewer foraging trips and gain more energy per trip. On the other hand, parents that forage near the central place would make many short foraging trips and return with lower energy per trip [170]. This theory has been tested in birds and otariids [171, 172].

The high concentration of nutrients in the milk is sufficient to sustain the pup while fasting on land during its mother's absence at sea [13, 31]. This is true for species that have among the longest foraging trips reported for any otariids such as the subantarctic fur seals, the Juan Fernandez fur seals, and the Guadalupe fur seals (**Figure 4** and **Table 6**). For females producing milk with high concentration of lipids when making long foraging trips, there must be physiological and reproductive advantages [27, 29, 35]. These advantages may include less pressure on water balance due to reduced need for water, and the capacity of the mammary gland is not a limiting factor when secreting milk with high solid content. Furthermore, the mechanisms regulating the milk secretion in which the mammary gland is able to resume lactation after long foraging trips (more than 12 days) and in the absence of the stimulus of the suckling pup and milk removal are unknown. The mechanism of milk secretion in terrestrial mammals, such as dairy animals, is controlled by autocrine factors and cell stretching [173, 174], but these are yet to be investigated in pinnipeds.

Otariid species that make long maternal foraging trips at sea may have limited capacity in their mammary gland in order to store great amount of milk.

An explanation is that the mammary glands might have a large storage capacity twosome with a slow secretion rate of high energy-rich milk while foraging at sea [5]. This argument is supported by the weak negative relationship between the foraging trip duration of lactating Antarctic fur seals and the milk secretion rate while at sea and by the positive correlation between milk secretion rate and the duration of pup attendance on land [3]. In addition due to the absence of the suckling stimulus and milk removal, which are crucial for the maintenance of mammary gland function in other species, the mammary gland may be at risk of involution [5, 29]. How otariids are able to contain the involution of the mammary gland in the absence of the suckling stimulus and milk removal is still not clear.

Mammary gland size in pinnipeds is estimated based on the mammary gland weight relative to body weight, indicating that most otariids have large mammary glands in comparison with terrestrial mammals [5, 29]. The mammary gland
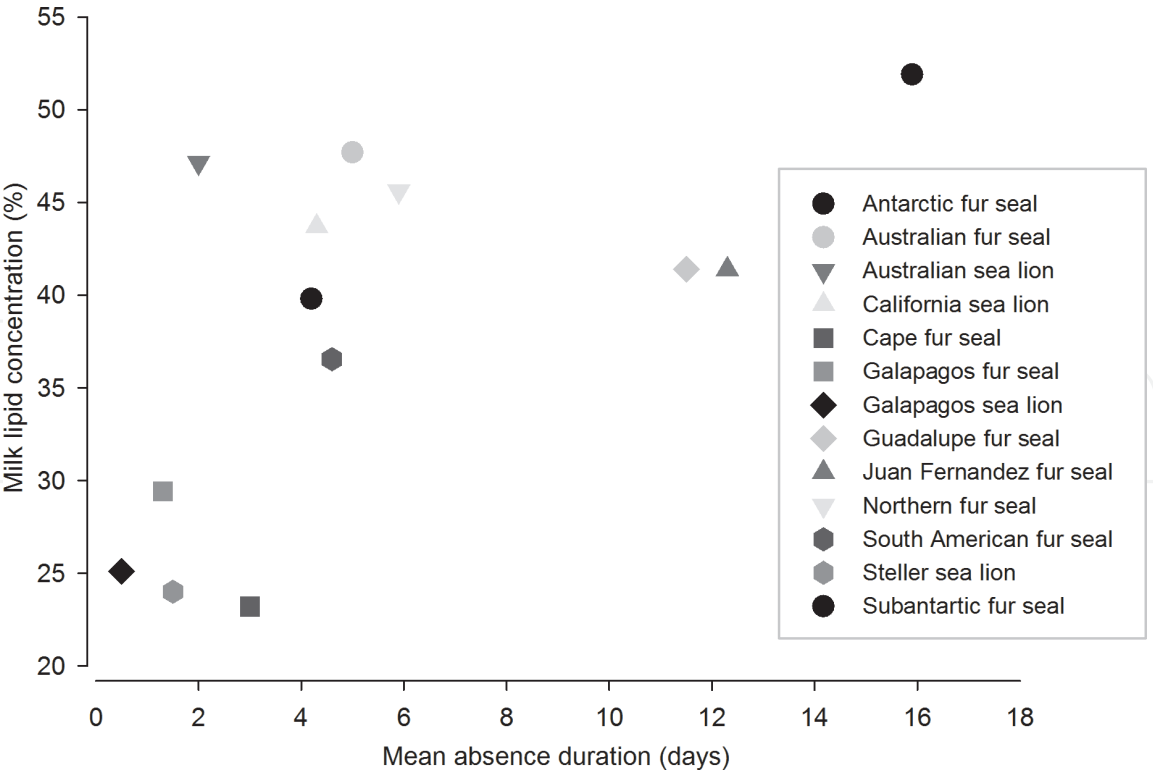
Figure 4.
*The relationship between foraging trip duration (mean absence duration in days) and milk lipid concentration in 13 species of otariids (data from sources in **Tables 4** and **6**). SL = sea lions, FS = fur seals.*

capacity of Antarctic fur seals was measured by complete manual evacuation and indicated that mammary glands were not completely full when the mother arrived ashore [31]. It is likely that the capacity of the mammary gland to store milk is not limiting the duration of foraging trips; however, it is possible that it is limited by a set point of the nutritional satiation reached by the mother [13].

The relationship between foraging trip duration and milk lipid concentration has been demonstrated between and within otariid species. The second of the two has been demonstrated in a few species. A significant relationship between milk lipid concentration and the duration of the preceding foraging trip in Australian and Antarctic fur seals was found [30, 31]. By contrast trip duration and milk fat content were not related in studies carried out on Australian [28] and New Zealand sea lions [82] and subantarctic fur seals [10]. The poor relationship found in subantarctic fur seals was thought to be a consequence of individual maternal foraging skills, and thus, the quality of the milk would have been determined by this factor [10].

Australian and New Zealand sea lions conform with the hypothesis that species that make short foraging trips secrete relatively low milk fat concentration [21, 82, 171]. Australian sea lions, as an adaptive response to inhabiting a low-energy marine environment, have prolonged the lactation period in which mothers have lowered the energy intake of their pup by secreting a low-energy milk [22]. Galapagos fur seals also produce a low-energy milk and have a foraging trip lasting 1.3 days and a prolonged lactation period (**Tables 1** and **6**). The duration of the foraging trips of lactating Galapagos fur seals appears to be regulated by short-term fluctuations of food availability [22]. Both temperate and tropical species, Australian sea lions and Galapagos fur seals, respectively, have adopted a different strategy to polar species in that they are obligated to extend their lactation period. As otariid

Species	Time to first departure (days)	Time absent (days)	Time presence (days)	Time absent (%)
Australian fur seal [30]	—	5.0 ± 0.1	—	—
South American fur seal [175]	—	4.6 ± 0.1	1.3 ± 0.1	78
Guadalupe fur seal [176]	—	11.5 ± 0.1	5.0 ± 0.1	70
Subantarctic fur seal [27]	—	15.9 ± 4.6	3.8 ± 1.1	81
Cape fur seal [43]	4.3 ± 3.3	3.0 ± 2.5	2.4 ± 1.4	56
California sea lion [19, 177]	5–8	4.3 ± 0.5	1.4 ± 0.1	75
Steller sea lion [37, 178]	5.8 ± 0.6	1.5 ± 0.1	0.86 ± 0.05	64
Galapagos sea lion [175]	6.8 ± 2.1	0.5 ± 0.1	0.6 ± 0.1	47
Antarctic fur seal [20, 23, 31]	6.9 ± 0.1	4.2 ± 0.8	1.8 ± 0.5	67
Galapagos fur seal [175]	7.4 ± 1.2	1.3 ± 0.1	1.0 ± 0.1	57
Northern fur seal [179]	7.4 ± 0.1	5.9 ± 0.1	2.2 ± 0.1	73
New Zealand sea lion* [180–182]	8.6 ± 0.2	1.7–2.7	1.2 ± 0.1	57–69
New Zealand fur seal [40, 41]	9.7 ± 0.1	4.2 ± 0.1	1.8 ± 0.1	70
Australian seal lion [1, 28, 183]	9.8 ± 1.8	2.0 ± 0.5	1.4 ± 0.3	59
Juan Fernandez fur seal [35]	11.3 ± 3.4	12.3 ± 0.1	5.3 ± 0.1	70

Attendance pattern were recorder at early lactation.

Table 6.
Temporal parameters of attendance pattern in otariids.

females depend upon their dietary intake to sustain lactation [135], and by regulation the duration of their foraging trips to food availability they are able to withstand a long lactation period. This strategy does not necessary occur at high latitudes in which the marine environment has dramatic rise in primary productivity during the short summer season and otariids are able forage successfully and complete lactation in a short period of time.

Subantarctic and Juan Fernandez fur seals inhabit lower latitudes, but contrary to other low-latitude otariids species, they conduct very long foraging trips (mean of 15.9 and 12.3 days, respectively) (**Figure 4**, **Table 6**). As would be expected for long forager trip species, they secrete milk with high lipid contents (38.6 and 41.4%, respectively). Moreover, these two species have one of the longest inter-suckling intervals and highest milk lipid concentration during the first month of early lactation among otariids [10, 29]. Both species leave their local low productive waters and travel long distances to waters of higher productivity [10, 35]. The similarity of the attendance patterns of Antarctic and subantarctic fur seals breeding at Macquarie island indicated that prey availability might be playing a major role influencing pattern of foraging and attendance cycles [9]. This was also shown to be true for Juan Fernandez fur seals that had a correlation between foraging trip, visit

duration ashore, and primary productivity, indicating that food source location and availability were determining the foraging pattern [35].

At least for some otariid species, long foraging trips are preceded by long nursing bouts ashore. At some point, when nursing the pup ashore, the energy needed to produce milk must come from body reserves; in this scenario the rate of milk secretion and rate of energy delivered to the pup would be dependent on the maternal body lipid storage capacity. In fact, 42–79% of the milk energy transferred to Antarctic fur seals' pup comes from maternal body reserves [31]. At least for this species, the longer the duration of the foraging trip, the greater the proportion of milk energy delivered to the pup is derived from body stores [31]. Probably the most beneficial cost-efficient lactating strategy would be to maximize energy transfer to the pups, by producing and storing an energy-lipid-rich milk while foraging at sea, and store excess nutrients as body lipids and protein to be used to secrete milk while nursing the pup ashore [31]. While ashore, the rate of nutrient transfer to the pup is maximized by increasing the milk production and the concentration of milk solids. Within otariid species two distinctive strategies of energy transfer to the pup can be identified, one that makes long foraging trips and maximized their energy transfer to the pup by secreting nutrient-rich milk and those species that makes shorter foraging trips and produce a low nutrient-rich milk (**Figure 4**).

There is a strong relationship between milk composition and attendance pattern in otariids in particular for species making long foraging trip at sea; however, for otariid species making short foraging trips, this relationship is unclear. Location of breeding site (latitude), distance between breeding site and foraging ground, and availability of food source may influence the attendance pattern of lactating females. The fact that lactating otariids are absent for the longest inter-suckling period of any of the mammals makes otariids an interesting group of mammals for testing the central place foraging theory [170].

4.3 Milk composition and stage of lactation

The general effect of stage of lactation on milk composition seems to be consistent across species [117, 184–188]; however, there are differences between species in the degree of change in the milk composition as lactation progresses.

4.3.1 Seals (phocids)

The fat content of the milk of phocids increases as lactation progresses, and pup growth rate reflects the extent of this increase (**Table 3**) [189]. Phocid offspring are not different from other mammalian species, and the demands for energy by the pup increase as lactation progresses [189], but how the increase in energy demand could influence the increase in milk lipid concentration has not yet been explained. Some phocid species secrete low-fat milk in early lactation, but protein concentration remains unchanged throughout lactation (**Table 3**). The low protein content in phocid milk is a consequence relatively small to the proportion of the gain in the young's lean body mass (**Table 3**). To give an example, hooded seals and bearded seals produce the lowest protein concentration of any mammalian milk [7, 97], and in hooded seal pups, the low protein content was associated with a low gain in lean body mass [74].

In phocids the concentration of water in milk decreases, and lipid concentration increases as lactation progresses [51, 61, 94, 96, 99–101]. Similarly, in harp seal milk, the protein content remained constant, and milk fat content increased

throughout lactation [94, 95, 106]. An explanation for the relatively high concentration of water in milk in early lactation is to provide the pup with water since the newborn cannot catabolize water from lipid reserves as an adequate body lipid layer (blubber) has not yet been formed. In consequence, milk provides free water to the pup when it is needed most, and the decline in water concentration in milk will coincide with the time the young is less dependent on free water [94].

Despite the short lactation duration in phocid, the pup is weaned with large weaning mass, and this is possible because the pup is nursed with very energy-rich milk and lipids are deposited rapidly in the blubber. Furthermore, in comparison with terrestrial non-fasting mammals, phocids have greater milk energy output rates [117]. Phocids are able to do so, due to the large maternal body mass that can store large quantities of energy in the form of lipids (blubber) which allow them to withstand the high cost of lactation by mobilization stored energy reserves [72]. However, some small body size phocid species such as harp seals, Weddell seals, bearded seals, and harbor seals feed at some stage during the lactation period [72, 74]. Harbor seals are known to feed from mid-lactation onward [73], most likely because energy reserves are depleted, and hence, they are unable to sustain lactation while fasting [72]. It appears that maternal size in harbor seals constrains the proportion of body fat that can be stored [73]. Furthermore, lactating harbor seals depleted 33% of their body mass during the first 80% of the nursing period and depleted their body reserves faster than other phocids [72]. A limited amount of energy stored coupled with rapid energy depletion during lactation cannot be sustained without feeding [69]. It has been suggested that it is likely that half of the phocid species may feed during lactation [6]; however, whether this occurs only in the smaller phocid species is still to be investigated.

In conclusion, lactating phocid produces great amount of energy in the form of very rich lipid milk that is transferred to the pup in a short time, and this energy is deposited as body reserves to be mobilized during the postweaning period. In addition, the pup is able to rapidly assimilate the lipid-rich milk and deposit the lipid in the blubber which is crucial for insulation and for postweaning energy reserves. The needs of the neonate seem to parallel the milk composition, and most phocids appear to follow the same trends. Some evidence has shown that not all phocid species are fast for the entire lactation period. Small body size phocids are unable to endure the cost of lactation and maternal metabolism solely with her body energy reserves and must forage to regain energy. These species of phocid have adopted an "otariid-like foraging strategy."

4.3.2 Sea lion and fur seals (otariids)

Data on changes in milk composition throughout the whole lactation period for 6 out of 16 otariid species have been investigated [2, 3, 5, 10, 30, 190]. The general trend in these species is that milk fat concentration increases progressively, whereas protein content remains fairly constant throughout the lactation period. Less complete, but otherwise useful, data are available from northern fur seals [191], New Zealand sea lions [82], Galapagos fur seals, and Galapagos sea lions [21].

Increase in foraging trip duration related to stage of lactation and/or change in food availability [1, 163, 164] may influence variation in milk composition during lactation. It is possible that there is a combination between the effect of stage of lactation and foraging trip duration on the composition of milk. Stage of lactation was responsible for most of the changes observed in milk composition of subantarctic fur seals [10]; however, in Antarctic fur seals and Australian sea lions, stage of lactation was responsible for only a small proportion of the changes in milk

composition [3, 28]. Kretzman et al. [28] and Gales et al. [2] found high variability in milk lipid concentration between and within individual Australian sea lions. However, they were unable to identify which factors contributed most to the variation in milk composition. In Antarctic fur seals, days postpartum and maternal mass contributed to the variation in milk lipid, and it was suggested that foraging trip duration also explained some of the variation [3]. These authors have recognized that extensive and systematic sampling is needed in order to describe milk composition in otariids and control for intraspecific variation in milk composition [3, 28].

The trend in changes in otariid milk composition during lactation is as follows: milk lipid and gross energy concentration increases during the first stages of lactation and peaks at mid-lactation and then decreases in the course of later stages of lactation (**Table 4**). Water content in milk changes inversely with milk lipid concentration, while milk protein concentration stays somewhat unchanged throughout the lactation period [10]. Although not all otariid species follow these trends, Galapagos fur seals, for example, produce milk that decreases in fat concentration with pup age in early lactation [21], and hence in the course of the perinatal period, they use their body fat storage to secrete lipid-rich milk. This has some advantages as the mother can conserve body water and the neonate is able to build up the layer of blubber that will act as insulation layer and energy reserve for the approaching period of fasting. The mother's water balance enhances at the start of the foraging trip, and on her return, she nurses the pup with a diluted milk that meliorate the pup's capacity to deal with the high temperatures at the Galapagos Islands [21].

Protein concentration in milk of Antarctic fur seals declined in 1 year but heightened in the following 2 years [3] but did not changed in Australian fur seals [30]. The increase of milk protein concentration during lactation may respond to the need to incorporate essential nutrient for pup growth. The proportions of the total protein in milk of whey and casein changed in the milk are produced by Galapagos fur seals at early and mid-lactation (40–25%, 60–75%, respectively) [83]. The reason and connotation for the changes in the proportions of whey and casein of the total protein in milk of Galapagos fur seals remain to be elucidated.

Increment in fat and energy concentration of milk at early lactation has been related with increment in the duration of foraging trips and/or the stage of lactation in some species of otariids [2, 3, 9, 30, 191]. However, in some species the foraging trip duration was not related to changes in milk composition; hence, it is possible that other mechanisms may be acting. After the long and energy-demanding perinatal period, the mother must replenish energy reserves and enhance body condition, in order to produce a higher-lipid concentrated milk at early lactation [18, 140]. Maternal body condition had a significant effect on milk lipid in subantarctic fur seals [10] and New Zealand sea lions [82], but it is not known whether this applies to other otariid species. The increasing demands of the growing pup may affect the maternal response and increase milk fat concentration [10].

By the last month of the lactation period, milk lipid content tends to decrease as shown in Australian sea lions and Australian fur seals and subantarctic fur seals [2, 10, 30]. In subantarctic fur seals, the data suggested that the relationship between milk lipid concentration and at the end of the lactation stage was best described by an asymptotic relationship, i.e., decrease in lipid content. The decrease in milk lipid concentration, i.e., lower rate of energy transfer to the pup, at the end of lactation could be associated with the proximity to the pup's weaning process and higher-energy demands of gestation [10, 30]. This argument was supported by a

study on subantarctic fur seals that showed that the mother directed their body reserves toward gestation and not to milk production [27].

For the Antarctic fur seals, the rate of milk production decreased by the end of lactation [192, 193]; however, a concurrent decrease in milk lipid concentration has not been reported in late lactation [3]. The short lactation period (4 months) in this species and mothers not actively gestating an offspring (delayed implantation) during this period put less pressure to meet the energy demands of lactation and gestation [194]. In this context the mother is able to allocate energy resources to milk production, and the quality of milk lipid remains unaltered [30].

5. General conclusion

There are three lactation strategies adopted by pinnipeds: a fasting strategy, foraging strategy, and aquatic strategy. Phocids have shortened the duration of lactation remarkably and reduced the time the pup and mother are exposed to the conditions of the terrestrial environments. Due to the shortage of lactation duration in phocids, the daily energy output is greater than in otariids, and phocids secrete very rich energy-dense milk. Producing milk high in solid content attenuates the impact of water stress in phocids' mother that is fasting during lactation. However, some phocid species with small maternal body size have adopted a strategy similar to that seen in otariids and feed during lactation probably due to the high-energy cost to sustain the short lactation period. Walruses have evolved to nurse and feed without separating the mother from the pup in the so-called aquatic lactation strategy. The lactation duration in walruses is very prolonged (up to 3 years) which increments the chances of pup survival. Otariids also have long lactation periods, and the rate of pup growth is slower than in phocids. The concentration of milk lipid ranges greatly among pinniped species, and the absence or presence of traces of lactose in their milk may be associated with the evolution of lactation strategy in pinnipeds.

The stage of lactation, attendance pattern, and maternal body condition are factors that influence the milk composition throughout the lactation in otariids.

In order to make interspecies comparison, the milk composition values at mid-lactation should be used, since they represent the peak maximum production [117] and be limited to species for which similar data are available [2]. Researches that have collected milk samples from lactating otariids throughout the lactation period are limited. Attempting to compare the milk composition among pinnipeds is a difficult task due to the lack and poor quality of the data, small sample size, and being unrepresentative of the whole lactation period.

Lactation is a crucial part of the life history of mammals and is of particular interest in pinniped as they have adopted unique lactation strategies among mammals. In order to study lactation, the milk composition and amount of milk secreted are important parameters that need to be measured adequately.

The data reviewed in this chapter has demonstrated that data on the milk composition of pinnipeds is limited but nevertheless valuable. And that there are logistical constraints working in remote field sites, and with wild animals such as pinnipeds making the collection of milk samples difficult. In addition different analytical methods have been used, and the effect of stage of lactation among other factors is often not considered or mentioned in the literature [5, 195]. In lactation studies of pinnipeds, the lack of extensive sampling has made interspecific comparisons difficult. For otariid species, milk composition has been analyzed throughout the entire lactation period (in only three species) [2, 10, 30] and for interannual variation [3, 82, 196].

The stage of lactation influences the milk composition in pinnipeds [117], but there are factors that may also affect its composition. Maternal reproductive success in pinniped, i.e., success in rearing her pup, is directly influenced by her performance during lactation, and the survival of the offspring depends on the quality (energy content) and quantity of milk produced by the mother.

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