Chapter 8
Reproductive Energetics of Phocids

Daniel P. Costa and Jennifer L. Maresh

Contents

Abstract Phocid seals have a highly derived reproductive strategy characterized by the separation of feeding and reproduction, oftentimes across considerable spatial and temporal scales. Seals spend an extended period of time foraging far from the breeding colony, building up their energy reserves for a relatively brief pupping season onshore where access to food is limited. During lactation, enormous amounts of energy are quickly transferred from mother to pup before an abrupt weaning. This unusual reproductive strategy enables phocids to utilize habitats unavailable to most other mammals that must feed during lactation, from the unproductive waters of the tropics to the unstable pack ice of the world's polar seas. In this chapter, we examine: the physiological, ecological, and behavioral adaptations behind the phocid breeding system; the ways in which resources are acquired and allocated to understand the importance of body size, lactation interval, milk energy content, and lipid stores in support of phocid reproduction; the connections between phocid mating systems and pupping substrate; and, finally, the origins and evolutionary implications of this extraordinary life history pattern.

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8.1 Introduction

The initial utilization of the marine environment by ancestral pinnipeds occurred at a time when coastal upwelling was at a cyclic high, resulting in an abundant, diverse, and essentially untapped food resource (Lipps and Mitchell 1976; Vermeij and Dudley 2000). While they were able to take advantage of the abundant marine resources, their terrestrial ancestry dictated they remain tied to shore for pupping. Phocid pups are born onshore or on ice and, for most species, largely remain there until they are weaned. In some species, the pups make short forays into the waters adjacent to the breeding colony, prior to weaning. As in most mammals, lactation limits females to be the sole caregiver, thus, lactating females must balance the time spent on shore with their pup with the need to acquire prey energy at sea. As male reproductive behavior is associated with optimizing the number of females inseminated, spatial and temporal separation of feeding from reproduction is necessary for both males and females (Bartholomew 1970). The constraints associated with balancing these conflicting energetic demands play a major role in determining the reproductive behavior of phocids (Costa 1993; Boyd 1998; Trillmich 2010; Stephens et al. 2014). Phocids are an ideal study system because reproduction occurs over a very defined interval and, for many phocids, all or most of the resources needed for maternal investment are contained within the female when she gives birth to her pup. As a result, the energy and material transferred between mother and pup are readily measured, making phocid reproduction one of the best-studied systems of all large vertebrates.

In the sections that follow, we consider the connection between habitat diversity and the diversity of phocid lactation patterns; the fitness advantages and energetic challenges of the capital breeding system; the origins and evolutionary implications of this reproductive strategy; and future directions for research into phocid reproductive energetics.

8.2 The Capital–Income Continuum

Phocids have evolved the highly derived “capital breeding” system, a reproductive strategy that is characterized by the complete separation of feeding and lactation (Costa 1991a, b; Schulz and Bowen 2005). For those species that are “pure” capital breeders, females conceive young during the previous reproductive season, and then spend an extended period of time foraging at sea for their own metabolic needs and those of the developing fetus, as well as laying down reserves (capital) for the short, but energetically intense lactation period of 4–35 days that follow parturition

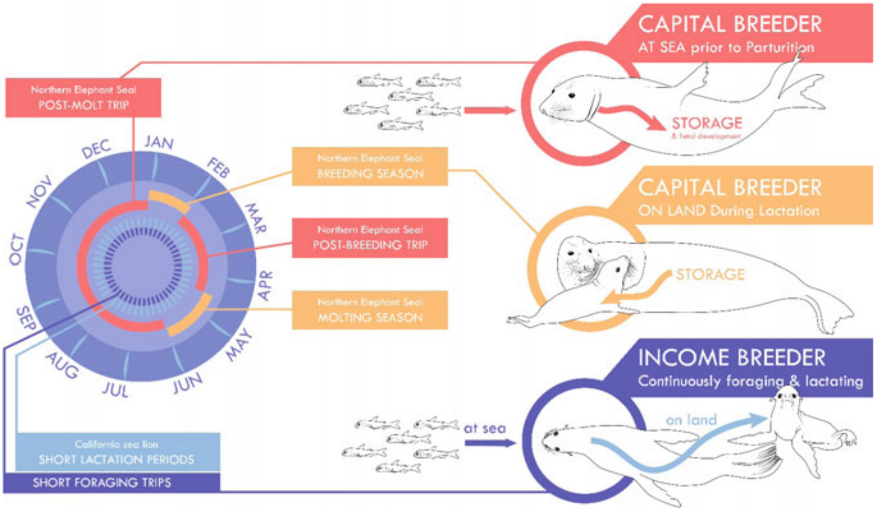

Fig. 8.1 The annual cycle of a capital breeder is compared to that of an income breeder. An income breeder feeds throughout the year and supports the growth of the pup from prey resources captured during intermittent foraging trips. Capital breeders spend extended periods at sea away from the breeding colony acquiring resources and then return to the colony to pup. During this period, the mother fasts and produces milk from stored resources acquired over the long foraging trip. Figure by Jessica Kendall-Barr

(Fig. 8.1; Schulz and Bowen 2004). For example, female northern elephant seals (*Mirounga angustirostris*) undertake one long foraging trip to sea, traveling over 3000 km from their breeding colonies to their feeding grounds. After 8 months of foraging at sea, they return to shore to give birth, where they are able to support a ~1-month-long lactation period without the need to return to sea to forage (Robinson et al. 2012). In this regard, female phocids are truly remarkable; lactation is so energetically demanding that, with the exception of bears and some marine mammals, no other mammal is capable of producing milk without feeding (Oftedal 2000).

The nutritional provisioning of young under the capital breeding system uncouples the need to travel to and from the foraging grounds during lactation, which allows individuals to utilize prey that is more dispersed, patchy, unpredictable, or distant from the breeding grounds (Costa 1993; Stephens et al. 2014). This uncoupling buffers populations against short-term fluctuations in habitat quality and resource availability. Not all phocids are "true" capital breeders and many species fall along a continuum between pure capital and income breeding. While elephant (*Mirounga* spp.), gray (*Halichoerus grypus*), Hawaiian monk *(Neomonachus schauinslandi*), and hooded (*Cystophora cristata*) seals are true capital breeders, species like Weddell (*Leptonychotes weddelli*), Mediterranean monk (*Monachus monachus),* harp *(Pagophilus groenlandicus),* ringed (*Pusa hispida*), and harbor (*Phoca vitulina*) seals include some degree of supplemental feeding during lactation, therefore relying on a certain amount of "income" during lactation (Hammill et al. 1991; Boness et al.

1994; Gazo and Aguilar 2005; Wheatley et al. 2006; Chaps. 9–10, , 12–14 and 16). As these species are constrained to remain nearby the nursing grounds, they cannot access all the advantages of capital breeding.

While some phocids exhibit supplemental feeding, the energy expended during lactation is primarily supplied by stored body reserves for all phocids except Mediterranean monk seals and possibly ringed seals. Body reserves are necessary as phocid mothers could not acquire sufficient energy foraging during the short lactation period to provide all of the energy necessary for both milk production and maternal maintenance metabolism (Schulz and Bowen 2005; Wheatley et al. 2008; Stephens et al. 2014). Supplemental foraging might be a way of meeting the additional cost of maternal metabolism associated with an extended lactation period and/or small body size.

The capital and/or supplemented capital breeding system made it possible for phocid seals to inhabit the less productive waters of the Caribbean and Mediterranean Seas, as well as the Hawaiian Islands, and to reproduce on ice, allowing them to colonize both polar oceans. The ability to remain with the pup throughout lactation influences a variety of behaviors discussed elsewhere, such as mother–pup interactions. For example, there is less selective pressure for females to be able to recognize their pups (Chap. 3), which may lead to the alloparental care reported in Hawaiian monk seals (Boness et al. 1998), and higher pup mortality when pups become separated from their mothers, as reported for elephant seals (Briggs and Le Boeuf 1975).

In contrast to the comparatively rare capital breeding strategy, the necessity of feeding during lactation and acquiring most if not all the energy required for lactation during this time characterizes most mammals and all other pinnipeds as "income breeders." Under this strategy, sustained milk production for young is supported by many short foraging bouts across a relatively long lactation period, constraining mothers to forage on resources close to their breeding colonies (Costa and Valenzuela-Toro 2021). The income breeding strategy thus couples reproductive success with local prey abundance (Costa 1993; Boyd 1998), creating a stronger link between local environmental fluctuations and population status (e.g., El Niño events; Trillmich et al. 1991; Costa 2008). As a result, income breeders tend to be limited to breeding in highly productive regions (Costa 1993; Costa and Valenzuela-Toro 2021). Otariids exemplify this income-breeding strategy, with lactation durations that can last upward of 2 + years (Trillmich 1990). For example, female California sea lions (*Zalophus californianus*) can make 50 trips to sea during an 11-month lactation period, typically spending 3–6 days foraging within 50–100 km of their breeding colonies (Fig. 8.2; Kuhn and Costa 2014; Costa and Valenzuela-Toro 2021).

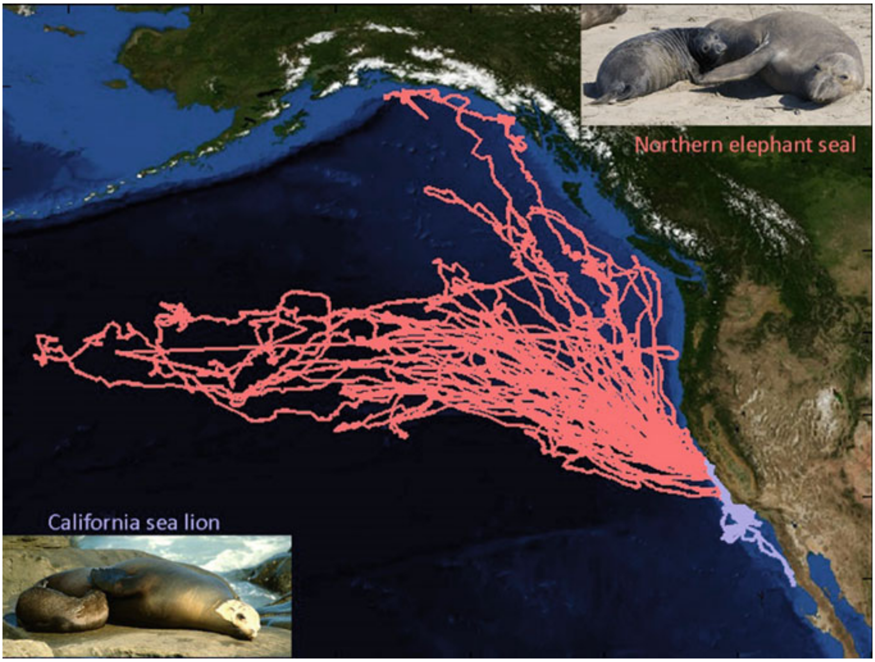

Fig. 8.2 Tracks of female northern elephant seals on their post-molt foraging trips traveling over 3000 km from the Año Nuevo colony (pink) compared to foraging trips of female California sea lions (purple) that are typically 85 km away from the San Nicolas Island colony

8.3 Habitat and Breeding Systems: Environmental Potential for Polygyny

Phocids can access prey resources in most habitat types found in the marine environment, including open ocean (e.g., elephant seals), coastal inshore habitats (e.g., monk and harbor seals), freshwater (harbor, Caspian *Pusa capsica*, and Baikal seals *Pusa sibirica*) and pack and fast ice habitats (e.g., hooded, harp, ringed, Weddell, and crabeater seals *Lobodon carcinophagus*), (Costa 1993; Schulz and Bowen 2004, 2005). In addition, the ability to rely on body stores to offset or entirely support the cost of lactation allows phocids to utilize a diversity of substrates for reproduction, from relatively fixed landmasses to unstable pack ice, giving rise to a variety of lactation strategies (see also Chap. 7).

Phocid seals exhibit the complete range of breeding systems observed within pinnipeds, ranging from the highly polygynous system of elephant seals, which exhibit some of the greatest sexual dimorphism observed in mammals (Fig. 8.3; Chap. 11), to serial monogamy with little or no dimorphism (many ice seals), to the polygynous reverse sexual dimorphism observed in leopard (*Hydrurga leptonyx*) and Weddell seals (Chap. 13). These different breeding systems follow the predictions

Fig. 8.3 The top image shows the extreme sexual dimorphism of a male seal copulating with a female northern elephant seal at the Año Nuevo Colony. Males weigh 1360–2270 kg compared to 400–770 kg for females. The bottom image shows two crabeater seals on an ice-floe. It is hard to tell the difference between a male and a female crabeater seal. Photo credits: D. Costa

of the Environmental Potential for Polygyny (EPP), where different habitat types are coupled with the reproductive behaviors best suited for the challenges and advantages of that environment (Emlen and Oring 1977; Trillmich 2010). Specifically, EPP predicts that breeding systems reflect the ability of males to control access to, and mate with, estrous females, which, in turn, is determined by the degree to which estrous females aggregate in space and time around critical resources. Phocids use land or ice for pupping, and the different characteristics of these breeding substrates—including abiotic factors such as substrate stability and access to the water, as well as biotic factors such as prey availability and exposure to predators—influences the degree to which females aggregate (Fig. 8.4; Le Boeuf 1991; Chap. 7).

8.3.1 Land-Breeding Seals

Islands and mainland beaches generally offer stable and relatively safe breeding grounds for phocids compared with some other habitat types; however, the availability of sites favorable for pupping can be limited (Fig. 8.4). Also, land-breeding females often have species-specific or even individualistic preferences for habitat characteristics, resulting in a tendency to aggregate in the most prime locations (Reiter et al. 1981; Cameron et al. 2007; Hadley et al. 2008). Together with estrous synchrony, these predictable aggregations allow males to mate with many females as well as defend them from rival males (Bartholomew 1970). Thus, the EPP is highest for species that breed on land, and we observe a breeding system that reflects this.

Land-breeding is relatively uncommon in phocids but includes both species of elephant seals and the gray seal—all excellent examples of high EPP for land-breeding phocids (Deutsch et al. 1990; Chaps. 9 and 11). The remaining species of land-breeding seals, which includes harbor seals and both species of monk seals, instead exhibit a slightly polygynous or serially monogamous breeding system. For these species, pupping occurs on land, but copulation occurs in the water (Johanos et al. 1994), so males have a more difficult time controlling access to estrous females.

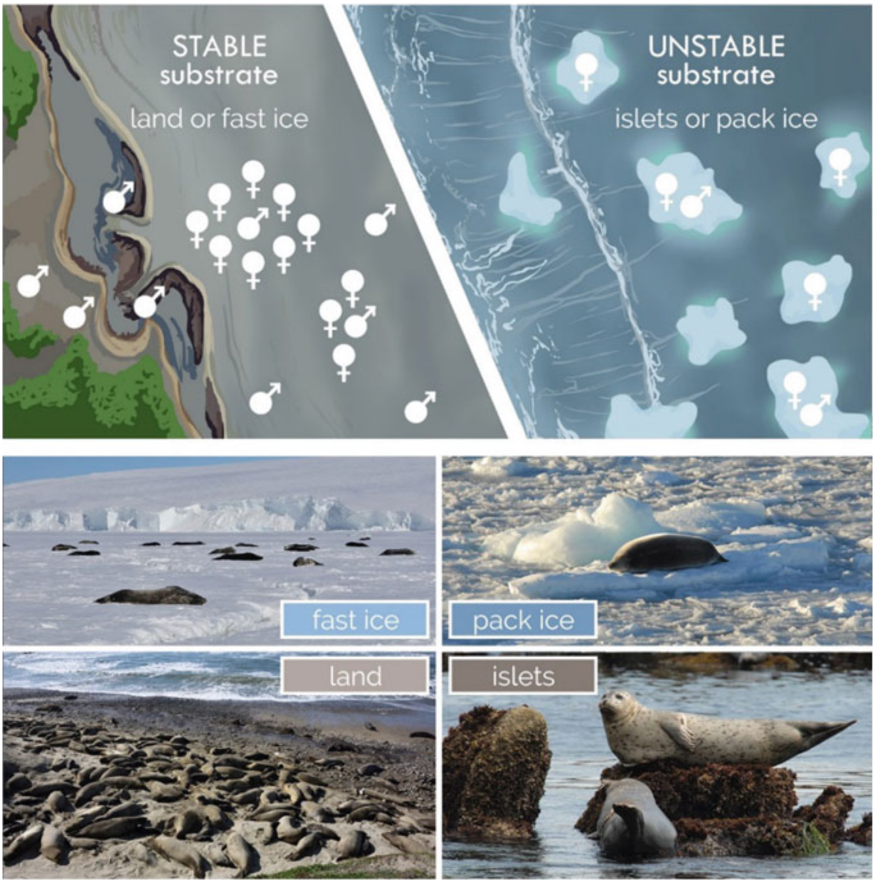

Fig. 8.4 Top left, a hypothetical example of a land-based breeding site where females form aggregations or "harems" in the center of the colony. A single male typically guards each harem. Subadult and subordinate males aggregate around the periphery of the harem. Top right, a hypothetical example of a pack ice breeding situation where the disbursed breeding substrate causes females to be disbursed. In this situation, a male can only guard one female. The bottom four figures are examples of fast ice breeding Weddell seals (upper left), a pack ice breeding crabeater seal (upper right), land breeding northern elephant seals (lower left), and an islet breeding harbor seal (lower right). Photo credits: D. Costa. Figure by Jessica Kendall-Bar

This results in a low EPP (Hayes et al. 2004), with reduced or even reversed sexual size dimorphism (females are the same size or larger).

8.3.2 Ice-Breeding Seals

Most phocids pup on ice, which is less stable and predictable than land, although the degree to which that is the case varies substantially between different types of ice (Fig. 8.4). At one extreme is pack ice, which consists of many small pieces of drifting ice that are widely dispersed and somewhat ephemeral. Most phocids breed on pack ice, including crabeater, leopard, hooded, harp, spotted (*Phoca largha*), Ross (*Ommatophoca rossii*), ribbon (*Histriophoca fasciata*), and bearded (*Erignathus barbatus*) seals. The other form is fast ice, expansive sheets of ice relatively fixed to land. Fewer species breed on fast ice but include Weddell, Baikal, Caspian, and ringed seals. Both types of ice—pack and fast—reduce the tendency of females to aggregate, although for different reasons. In addition, copulation between ice-breeding seals usually takes place in the water, where the ability of males to control access to estrous females is limited. Thus, the EPP is low for ice-breeding species, and sexual dimorphism is, in most cases, reduced or absent; however, the details of each breeding system are dictated by the specific characteristics of the substrate.

In species that breed on pack ice, females are widely dispersed and are generally observed alone with their pup or in a triad (a male and female with her pup). However, some species form large, loose breeding aggregations (Lydersen and Kovacs 1999). As pack ice is unstable and may disappear, females give birth during the short time when the pack ice is most stable and have a very short lactation interval to reduce the threat to newborn offspring. For example, hooded seals give birth and wean their pups in 4 days, while harp seals wean their pups in 12 days (Lydersen and Kovacs 1999). Upon weaning, females come into estrus synchronously, but briefly, which, together with the degree of spatial separation, limits the ability of males to mate with multiple females. However, serial monogamy may be possible where a male guards a female until she comes into estrus, mates with her, and then deserts her as he attempts to find unescorted, pre-estrous females (Bowen et al. 1985; Boness et al. 1988; Kovacs 1990). The difficulty of observing pack ice seals has led to far fewer observations of their breeding and copulatory behaviors when compared with phocids that breed on land. As a result, the degree of polygyny is challenging to assess. However, the consistent trend is for males to be slightly larger than females, suggesting slight polygyny or serial monogamy (Le Boeuf 1991).

Seals that breed on more stable fast ice are generally found in well-spaced colonies where females aggregate in small-to-moderate-sized groups with their pups (Fig. 8.4; Siniff et al. 1977; Bartsh et al. 1992). The limited availability of reliable cracks and holes in the fast ice that provides females access to the water facilitates the formation of these reproductive colonies. Individual males can establish an underwater territory and “resource guard” a crack or hole against rival males, thereby increasing the EPP compared with pack ice-breeding species. However, reproductive synchrony, in combination with these loose, well-spaced aggregations, makes it more difficult for males to monopolize either females or reproductive habitat when compared to land-breeding seals. This is generally the situation in the Antarctic; in the Arctic, predation pressure from polar bears further limits the aggregation of females on the fast ice, bringing the EPP closer to the pack ice end of the scale. Regardless of hemisphere, the predominant mating strategy for fast ice-breeding seals is serial monogamy or moderate polygyny.

8.4 Energy Acquisition and Expenditure Relative to Reproductive Patterns

An examination of how energy flows through an organism provides a mechanism to quantitatively assess the effort an animal spends acquiring resources and how those resources are allocated. Energy flow can be described as what goes into the animal as food and what comes out in the form of growth, reproduction, repair, mechanical work, and waste (Fig. 8.5). In the steady state, animals maintain constant mass, and the energy consumed is equal to the energy expended. In this situation, ingested energy remaining after fecal and urinary losses—metabolic energy (ME)—is expended in support of homeostatic maintenance of body functions (basal metabolism, thermoregulation) and in the further acquisition and processing of prey (mechanical work for

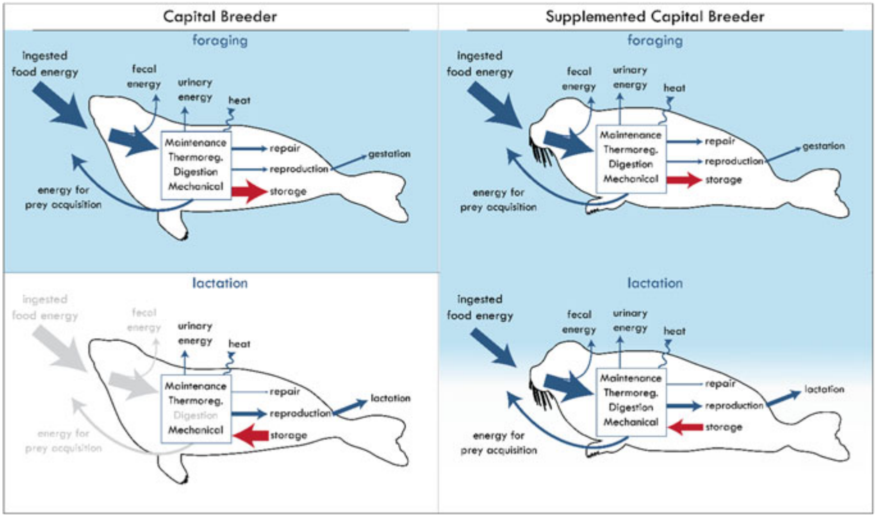

Fig. 8.5 A comparison of energy flow in reproductive female phocids, showing the differences between capital breeding and supplemented capital strategies. On the left, a capital-breeding phocid seal alternates between (top panel) positive energy balance while foraging at sea, and (bottom panel) negative energy balance while fasting onshore during the breeding season. While foraging, surplus energy is used in support of fetal gestation and in the buildup of maternal fat stores (capital; red arrows) that are later used in support of milk synthesis and metabolic overhead during a brief but energetically intense lactation period. On the right is a phocid mother who supplements maternal fat stores (capital; red arrows) with some degree of feeding (income) during the breeding season to sustain milk production across a relatively long lactation period

foraging, digestion of tissue). When more energy is consumed than is expended as ME, the surplus is used for growth, storage, or reproduction; this surplus is stored as an increase in body tissue, and the animal gains mass (positive energy balance). When the energy consumed does not meet ME, an animal will utilize the energy stored as body tissue and lose mass (negative energy balance). There is thus an ongoing tradeoff between energy in and energy out, and whether there is excess energy that can be used for storage, growth, or reproduction. Therefore, growth and reproduction require an animal to acquire more energy and nutrients than are necessary to support maintenance.

The rate of prey energy acquisition is directly related to the availability and quality of prey, and how it is distributed in time and space. As prey availability and quality decrease, the cost of finding prey increases, and a greater proportion of time (and therefore energy) is expended searching for prey (Costa 2008; Benoit-Bird et al. 2013a, b). Capital and supplemental capital breeders undergo periodic fluctuations in this dynamic equilibrium. They gain significant amounts of energy while feeding in highly productive environments over short periods, or while feeding on patchy or more dispersed prey over more extended periods, followed by prolonged negative energy balance while fasting during migration or reproduction (Costa 1993; Trillmich and Weissing 2006; Stephens et al. 2014).

As capital or supplemented capital breeders, phocids draw from stored energy reserves (i.e., metabolize fat) accumulated during an extensive foraging season to support all (pure capital) or most (supplemented capital) of the energy expended during a relatively brief lactation period. For this strategy to work, individuals must appropriately allocate acquired energy between the competing biological interests of survival, growth, and reproduction, as they are limited by the finite amount of resources available to them in their environment.

8.4.1 Energy Allocation to Growth and Reproduction

In female phocids, as in other mammals, reproductive costs are associated with an investment in offspring growth through gestation and lactation. Gestation costs come in the form of the energy contained in fetal tissue, as well as the energy to fuel the metabolic processes associated with gestation—a.k.a., the "heat of gestation" (Brody 1945). Lactation costs come in the form of the energy and nutrients contained in milk, as well as the energy to fuel milk synthesis. Maternal energy reserves must also be used in support of the mother's maintenance metabolism during lactation—a.k.a., maternal "metabolic overhead" (Fedak and Anderson 1982). While there are no measurements on the heat of gestation in marine mammals, maternal metabolic overhead is relatively well studied, and we devote an entire section to discussing it below (see sect. 8.3.3). As metabolic overhead is considered a cost separate from energy spent on lactation per se, here we focus our discussion of lactation costs associated with the energy and nutrients contained in milk.

8.4.2 Milk Production and Lactation Duration

The relative investment of phocid mothers in their young via gestation and lactation can be appreciated by comparing pup mass at birth and at weaning to that of other carnivores. After a relatively long gestation period, phocid pups are born larger as a proportion of maternal mass (3.5–16.5%) than other carnivores (0.5–3%), indicating that phocid mothers invest more time and energy into fetal development (Figs. 8.6 and 8.7). Despite similar gestation durations, phocid mothers devote much less time toward offspring growth post-parturition than other carnivores (Fig. 8.7). For their body size, phocids have the shortest lactation period of any mammal, ranging from 4 days (hooded seals) to about 6–7 weeks (Weddell seals) before the pup is abruptly weaned (Bowen et al. 1985; Gazo and Aguilar 2005). Interestingly, Mediterranean monk seals are exceptional in that they wean their pups gradually over 4–5 months, more like an otariid than other phocids (Aguilar et al. 2007). Over the short lactation period, mothers transfer considerable amounts of energy to their pups, losing up to one-third of their postpartum mass to support accelerated pup growth (Crocker et al. 2001; Lydersen and Kovacs 1996; Mellish et al. 2000; Wheatley et al. 2006). For example, during their brief 4-day lactation period, hooded seal mothers transfer 10 kg of milk per day to their pups, which in turn, gain 7 kg per day in mass (Iverson et al. 1995). As a result of rapid energy transfer and an accelerated pup growth rate, phocid mothers can wean their young at a size comparable to that of other carnivores despite the short lactation interval (Fig. 8.7).

Lipid-rich milk facilitates the rapid delivery of energy to the pup, allowing species with the shortest lactation intervals to have the highest rates of milk energy delivery (Fig. 8.8). The fat content of phocid milk ranges from 24.5% in harbor seals to 65% in hooded seals (Oftedal et al. 1988), whereas most terrestrial mammals produce milk relatively low in fat. For example, cows and humans produce milk containing 4 and 8% fat, respectively. There are disadvantages to the high-fat content of phocid milk, as it is achieved by a reciprocal decrease in water content, with no corresponding change in protein content. Therefore, the protein-to-energy ratio of pinniped milk is lowest in the most energy-dense milk, and, while pups may receive enough energy to support their metabolism over the postweaning period, relatively little protein is provided for the growth of the lean body. As a result, by the time of weaning, the protein content of hooded, harbor, and gray seal pups has increased by 3, 10, and 11%, respectively, compared to an increase in fat stores of 82, 52, and 58% (Oftedal et al. 1993). Thus, species with extremely short lactation intervals have the least amount of lean tissue growth. For many species, such as elephant seals and Weddell seals, once pups are weaned, they undergo a postweaning fast that allows them to further develop their physiological capabilities, including their osmoregulatory and diving abilities (Adams and Costa 1993; Thorson and Le Boeuf 1994; Burns and Castellini 1996; Burns et al. 1997; Burns 1999). In addition to needing to develop their oxygen stores, the high proportion of adipose tissue would make pups relatively buoyant, further decreasing their diving ability. Finally, it is unclear how suckling pups maintain water balance given the low water content of their milk (Fig. 8.9).

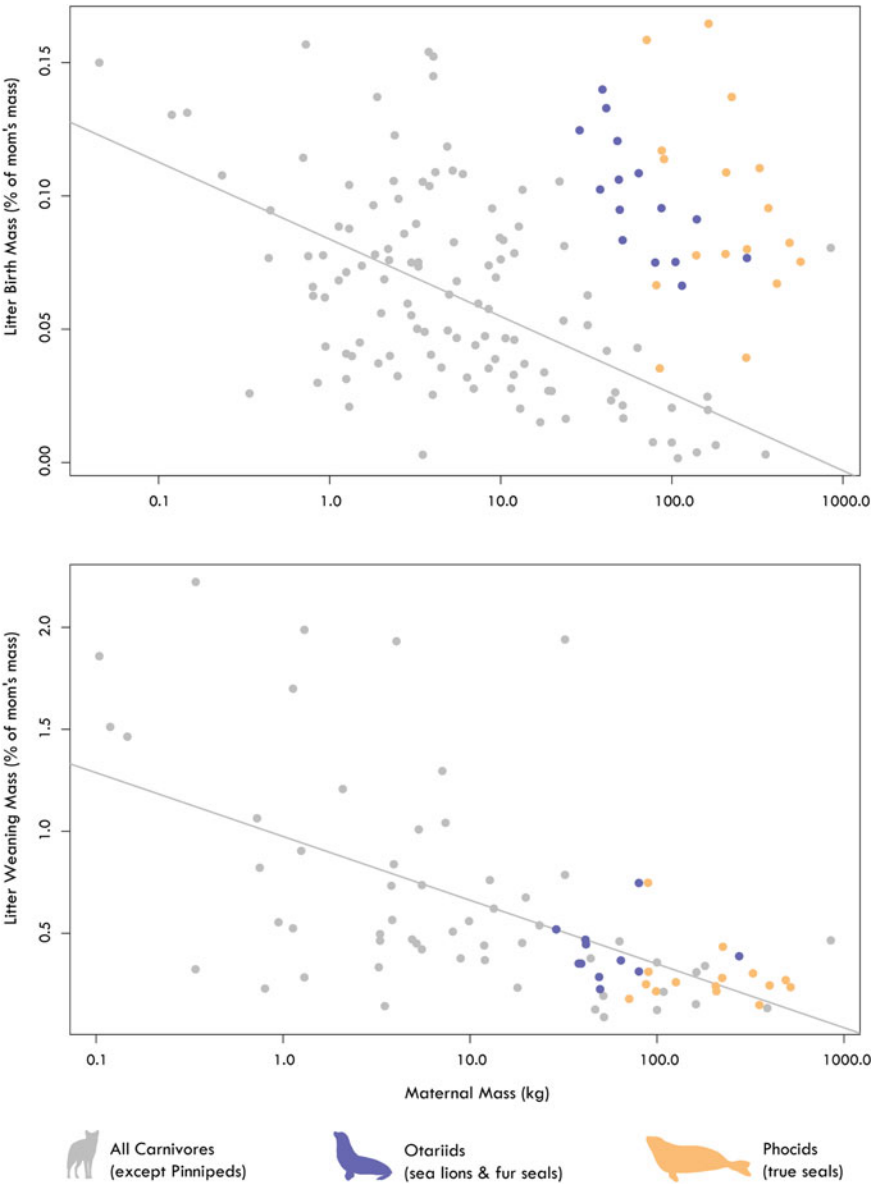

Fig. 8.6 The top panel shows the litter mass of Carnivora pups at birth compared to maternal mass. The bottom panel shows the litter mass at weaning for carnivores relative to maternal mass. Litter mass is the combined mass of all pups born in one parturition. Phocid (and otariid) females invest more in their pups at birth, but weaning occurs at similar weights to other carnivores

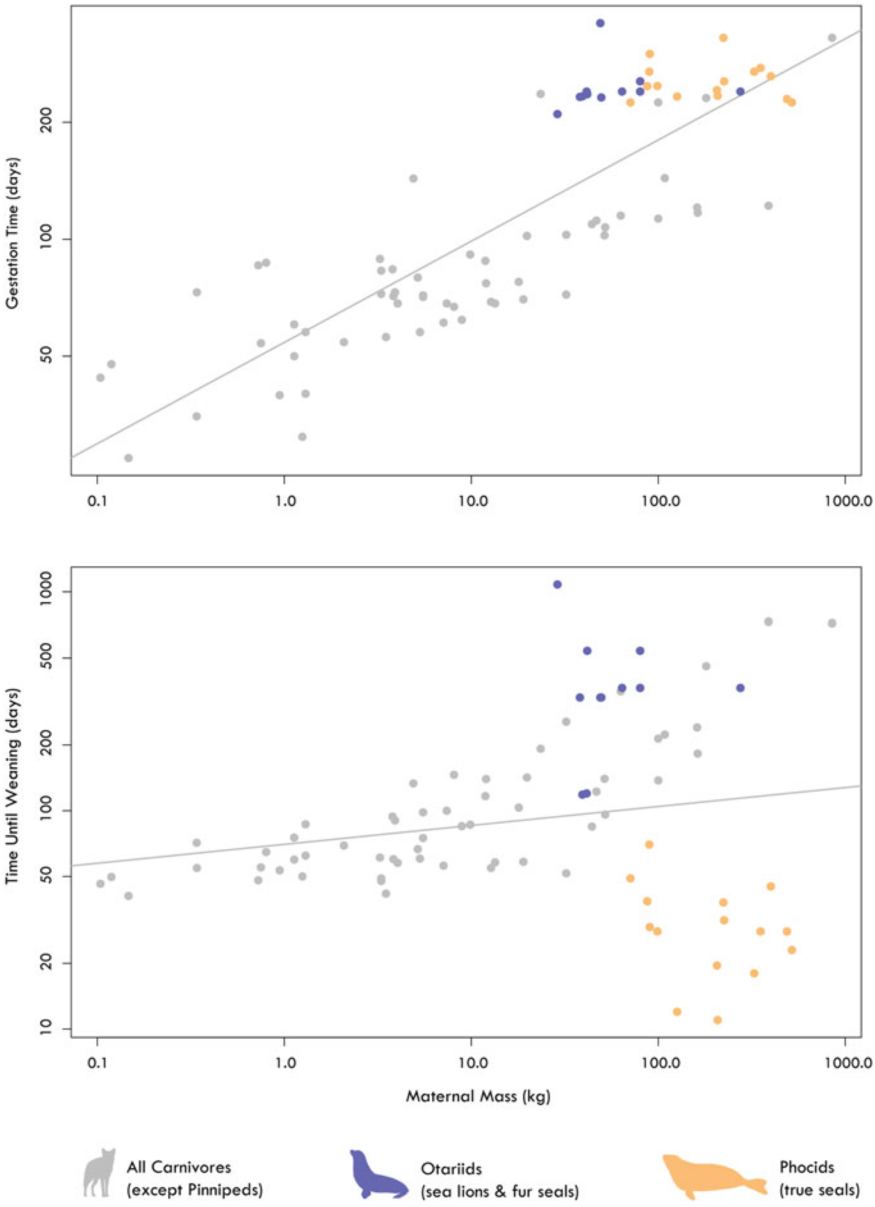

Fig. 8.7 The top panel shows the duration of gestation, and the bottom panel shows the lactation duration relative to maternal mass for carnivores. Compared to other carnivore species, phocid mothers have a longer gestation duration (top), but a much shorter lactation duration (bottom)

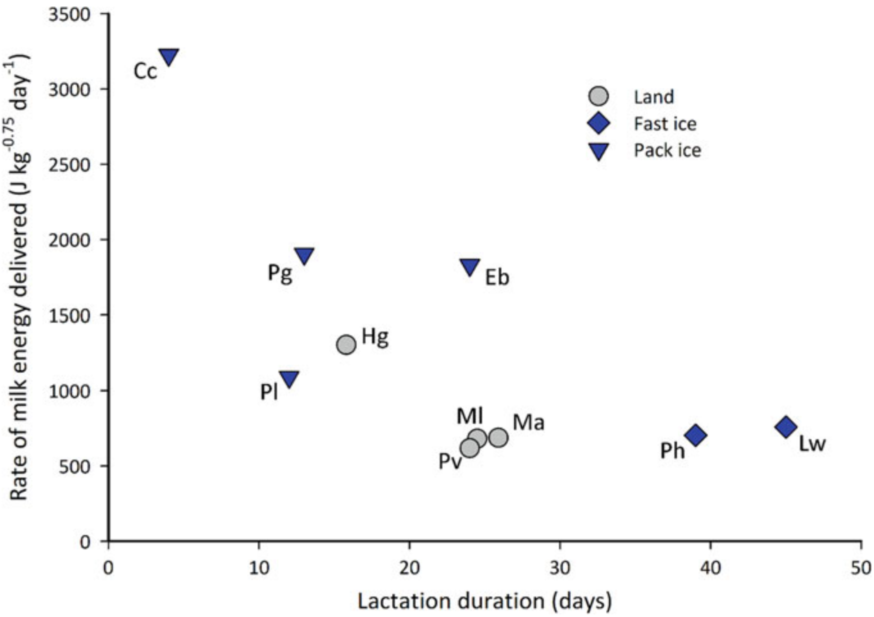

Fig. 8.8 The rate of milk energy provided to the pup compared to the duration of lactation. The rate of energy delivery normalized for differences in female body mass by dividing the absolute amount of energy in J delivered per day by female body mass raised to 0.75. The type of breeding substrate is also delineated for each species and are Ma = *Mirounga angustirostris*, Ml = *Mirounga leonna*, Pv = *Phoca vitulina*, Ph = *Pusa hispida*, Pg = *Pagophilus groenlandicus*, Hg = *Halichoerus grypus*, Pl = *Phoca largha*, Eb = *Erignathus babatus*, Cc = *Cystophora cristata*, Lw = *Leptonychotes weddelli*

Given the different lactation patterns exhibited in phocids, we might expect the total energy gained by pups to be quite variable; in fact, the energy gained by phocid pups is quite similar. What is different is how that energy is provided. For example, hooded seal pups are born with almost twice as much fat as other seal pups (14%) compared to harbor (10%), elephant (9%), gray (6%), and harp (3%) seal pups. They receive slightly less energy during lactation (13 MJ/kg$^{0.75}$ compared to 15 MJ/kg$^{0.75}$ for gray and harbor seal pups), but are still weaned with a fat content of 44%, which is similar to that of elephant (48%), harp (47%), gray (40%), and harbor (37%) seal pups (Kretzmann et al. 1993; Oftedal et al. 1993, 1996).

8.4.3 Body Size and Maternal Resources: The Role of Maternal Overhead

The ability of a female to fast while providing milk to her offspring is related to the size of her energy and nutrient reserves, and the rate at which she utilizes them.

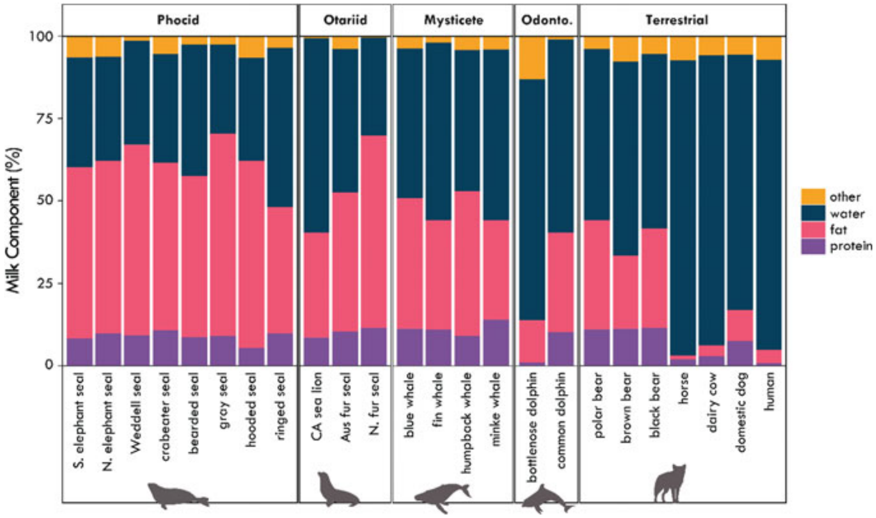

Fig. 8.9 A comparison of milk content across mammalian groups. Fat content is highest in capitally-breeding phocids, mysticetes, and bears. The high-fat content of phocid milk allows for the transfer of considerable amounts of energy to pups during a brief lactation interval. Note: polar bears (*Ursus maritimus*) are considered marine mammals but are shown in comparison to other bears

Reserves come in the form of fat stores, and female seals average 34% fat at or near parturition, with a range from 24.3% in harbor seals to 40.2% in Weddell seals (Bowen et al. 1992; Wheatley et al. 2006). This compares to a fat content ranging from a low of 9% to a high of 28% in terrestrial carnivores (Pond and Ramsay 1992). Fedak and Anderson (1982) coined the term "metabolic overhead" to define the amount of energy a female seal expends on herself while on land nursing her pup (Fig. 8.10). Metabolic overhead is relatively lower in larger animals because maintenance metabolism (energy demand) scales as mass$^{0.75}$, while fat stores (energy supply) scale as mass$^{1.0}$ (Kleiber 1975). Thus, large females can provision their young from stored body reserves for longer than small females. For example, the larger body size of older, more experienced northern and southern elephant seal mothers is associated with lower maternal metabolic overhead (see below), which allows them to provide more milk to their pups (Fedak et al. 1996; Crocker et al. 2001). Similarly, younger, smaller Weddell seals that have a higher proportional metabolic overhead spend more time foraging away from their pups than older, larger females (Wheatley et al. 2008).

The relationship between metabolic overhead, milk production, and lactation duration in a capital breeder was examined using a data-driven empirical model based on elephant seals (Costa 1993). This work was followed by mathematical optimization models that compared a fur seal to an elephant seal (Boyd 1998), an extension to a range of body sizes (Trillmich and Weissing 2006), and an examination of the role of food supply (Stephens et al. 2014). Together, these models show that a phocid mother can reduce her metabolic overhead by reducing the duration

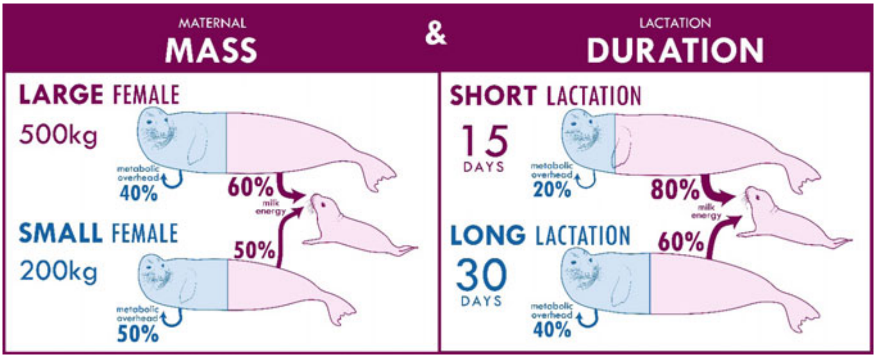

Fig. 8.10 Illustration of the importance of body size and lactation duration on the ability of the mother to invest her stored resources as milk energy to the pup. Larger females, and females with a shorter lactation period, have lower metabolic overhead. They are, therefore, able to provide a higher proportion of their stored energy to the pup as milk. Figure by Jessica Kendall-Bar

of lactation and/or by increasing her body size, thereby increasing the proportion of stored energy she provides her pup (Fig. 8.10). Thus, shorter lactation intervals allow a phocid mother to devote more energy to milk production rather than maintenance and, given the same lactation interval, larger females should have a lower metabolic overhead than smaller females.

The interaction between body size and lactation duration and its effect on metabolic overhead can be seen by comparing species along a continuum of lactation intervals. For example, the extremely short 4-day lactation interval of hooded seals results in a very low metabolic overhead of 27% (Mellish et al. 1999b). In contrast, elephant seals, the largest seal, have the next lowest metabolic overhead of 40% (lactation duration ~26 days (Costa et al. 1986; Hindell and Slip 1997). Gray seals are intermediate in size and have a metabolic overhead of 45% across the 16-day lactation period (Mellish et al. 1999a). Weddell seals have the most prolonged lactation interval studied so far (with respect to metabolism). They have a metabolic overhead of 54.9%, at least during the first 3 weeks of lactation when they are fasting (Wheatley et al. 2008).

As large body size confers an advantage in fasting ability, it follows that females that are ecologically constrained to being small must have short lactation intervals or must feed during lactation. For example, the need to avoid predators likely constrains ringed seals to be small so that they can hide from polar bears (Chap. 15). Similarly, harbor seals must be small enough to occupy small coastal islets and intertidal rocks to avoid predation by bears and wolves (Schulz and Bowen 2004). Both ringed and harbor seals feed during lactation, but as resources are nearby where they pup, they can do this. However, when ecological conditions favor large body size (or at least do not disfavor it), a longer lactation interval is possible while still fasting, if not adaptive. For example, as elephant seals breed on islands devoid of land predators, there is no pressure to be small and hide. This coupled with the ability to forage far from the colony at great depths, makes their large body size quite adaptive.

While there are no land predators in the Antarctic, killer whales (*Orcinus orca*) and leopard seals are effective marine predators (Siniff and Bengtson 1977; Guinet 1992; Pitman and Durban 2012). The potential impact of aquatic predators on the life history patterns of phocids requires further investigation. Nevertheless, the fast ice breeding colonies of Weddell seals are free from any form of predation, at least during the reproductive period until the fast ice breaks up in the late summer (Chap. 13). Large body size also improves diving ability and is discussed below (see Sect. 8.5).

8.5 Constraints on Body Size

Large body size is generally an advantage under the capital breeding system; however, there are factors outside of reproductive considerations that limit phocid body size, such as thermoregulation, locomotion, and patterns of prey availability. Thermoregulatory constraints put a lower and upper limit on body size due to the relationship between an animal's surface area to volume ratio and rates of heat transfer (Schulz and Bowen 2005). Smaller organisms lose heat faster than large organisms due to a higher surface area to volume ratio; therefore, given the high heat capacity of water, there is a limit to how small an endothermic, aquatic mammal can be (Clauset 2013). Conversely, as pinnipeds must periodically return to land, they face the opposite problem while onshore of needing to be able to offload heat, which is constrained by a large body with excellent insulation optimized for reducing heat loss while at sea (Bartholomew and Wilke 1956; Boness and Francis 1991; Norris et al. 2010; Codde et al. 2016). Thus, given the low heat capacity of air, there is a limit to how large a well-insulated mammal on land can be.

Locomotory considerations also constrain phocid body size. On land, the reproductive advantages of being large come at the expense of locomotor performance due to the morphological compromises associated with their amphibious lifestyle (Fish 2000). Biomechanical models show that the mechanical energy expended while traveling over land is disproportionately greater ("exorbitantly high") in the largest male elephant seals compared to that of smaller phocids such as gray and harbor seals (Garrett and Fish 2015; Tennett et al. 2018). Conversely, in the water, extreme size is generally associated with improved swimming economy and greater diving ability; however, the deposition of the fat stores necessary to sustain reproduction on land (i.e., fattening) can cause animals to deviate from the optimal, streamlined shape that minimizes drag in swimming animals (Fish 1994; Stephens et al. 2014). Fat stores also impact swimming costs via their effect on buoyancy (Stephens et al. 2014). For example, female elephant seals exert greater effort during diving when they deviate from neutral buoyancy as they increase or decrease their fat stores (Adachi et al. 2014).

Finally, patterns of prey availability also place limits on body size. While larger animals are more energetically efficient on a mass-specific basis (i.e., they require less prey for a given mass), they nevertheless require more prey as they are larger. This relationship has been examined in optimality models (Boyd 1998; Trillmich and Weissing 2006), which have shown that, for a given travel time, small animals could successfully subsist on a lower prey availability than large animals. In contrast, a more recent modeling effort found that increases in food availability, seasonality, and to a lesser extent, the unpredictability of prey, all favor the capital breeding system and, thus, large body size (Stephens et al. 2014). While these modeling efforts are quite insightful and have provided support for some of the factors related to food availability that lead to the evolution of a capital breeding system, they are limited in the processes they can examine (Trillmich and Weissing 2006). For example, the physiological processes that determine the rate at which prey and milk can be processed will constrain time at sea and lactation duration, respectively. Mothers can only deliver milk as fast as the pup can consume and process it, and the maximum rate at which a female can feed is limited by her ability to digest and process prey. Interestingly, compared to terrestrial carnivores, pinnipeds have longer intestines that allow them to process prey faster, making it possible for them to forage more frequently (Williams et al. 2001; Williams and Yeates 2004).

The effect of prey availability on body size has been well studied in ringed seals (Ferguson et al. 2018). This species generally exhibits a reproductive strategy with more income breeding traits than most phocids, having a smaller body size and, therefore, less capital available to transfer to their young. They also inhabit a large latitudinal range with highly varying climate and resource conditions; individuals at the northern end of the range experience greater variability in climatic conditions, which should favor larger (more efficient) body size to buffer against poor food availability and unpredictable timing of ice break-up (Ferguson et al. 2018). As predicted, a latitudinal gradient in body size has been reported for ringed seals, with an overall larger body size and reverse sexual dimorphism seen in more northern populations (Ferguson et al. 2018, 2019). In essence, ringed seals exhibit a within-species latitudinal gradient along with the capital–income spectrum whereby northern individuals exhibit stronger capital breeding traits than their more southerly counterparts (i.e., more frequent skipping of a reproductive cycle, slower growth rates, and larger size at maturity; Ferguson et al. 2019).

8.6 Foraging and Reproduction: An Economical Lifestyle

Optimization models have shown that capital breeding will emerge when the correct set of environmental parameters are in place (Boyd 1998; Trillmich and Weissing 2006; Stephens et al. 2014). These models assumed that the cost of existence for capital and income breeders is equivalent, but empirical data suggest otherwise. Income breeding otariids have higher maintenance and field metabolic rates than capital breeding phocids (Maresh et al. 2014; Costa and Maresh 2018). Costa (1991a) hypothesized that capital breeders would have lower metabolic costs (mostly associated with activity costs) because, with spatial and temporal separation of breeding from feeding, the mother is released from having to return to the pup in a timely manner. This system promotes energetically conservative foraging behaviors in capital breeders. For example, the ability to utilize highly dispersed or distant prey resources is improved by traveling to and from those resources economically (e.g., slow and deliberate flipper stroking, (Adachi et al. 2014; Maresh et al. 2014). The conservative lifestyle of phocids extends to the way that they quietly surface and descend while swimming (Costa 1991a; Williams and Maresh 2015), a pattern quite different than that observed in otariids. Economical travel reduces at-sea metabolic rate and overall energy expenditure, thereby increasing the amount of energy available for reproduction (Maresh et al. 2015).

Moreover, making a single long foraging trip increases the time available to forage and reduces the time spent in transit. Thus, by spreading the cost of reproduction (milk production and maternal metabolism) over a long trip to sea, a northern elephant seal female, for example, only has to increase her daily prey consumption by 12% (Costa et al. 1986) to gather sufficient energy to support herself and her pup on shore. This compares to an increase of 1.6 times (160%) the prey intake of a lactating compared to non-lactating female northern fur seal (*Callorhinus ursinus*; Perez and Mooney 1986).

Together with large body size, economical foraging, and a reduced at-sea metabolic rate increase diving ability by increasing a seal's aerobic dive limit (Ponganis 2016), allowing seals access to prey at greater depths (Chap. 4). As air breathers, foraging marine mammals are physiologically constrained during breath-hold by the amount of oxygen they have stored in their tissues compared to the rate at which this oxygen is utilized. Oxygen storage capacity increases with body size; therefore, just as metabolic overhead is constrained by body size, so is diving ability. Like the scaling of energy supply and demand described above, metabolic rate (oxygen demand) scales to body mass$^{0.75}$ whereas oxygen stores (supply) scale with body mass$^{1.0}$. More massive seals, therefore, have a lower mass-specific metabolism for a relatively constant proportion of oxygen storage capacity (Ponganis 2016). All things being equal, large mammals should be able to dive longer and deeper compared to smaller mammals based on body size alone.

Pure capital breeding phocids, such as elephant seals, have a reproductive pattern that is ideally suited for dealing with dispersed or unpredictable prey or prey that is located at great distances from the rookery or at great depth. Access to these resources is optimized by their large body size and elevated oxygen stores, coupled with the adoption of energetically conservative foraging and traveling behaviors that keep at-sea metabolic rates low. As a result, elephant seals are exceptional divers, comparing favorably with beaked and sperm whales as the deepest and longest diving mammals (Ponganis 2016).

8.7 Male Reproductive Energetics

In most mammals, males do not invest energy in parental care of offspring; instead, the cost of reproduction is associated with finding and maintaining access to estrous females and with inseminating as many females as possible (Deutsch et al. 1990;

Tinker et al. 1995; Kovacs et al. 1996; Coltman et al. 1997, 1998; Beck et al. 2003). For some phocids, this necessitates a substantial investment in growth, as large body size confers an advantage in antagonistic interactions (Anderson and Fedak 1985; Haley 1994). In addition, large body size is advantageous for territory maintenance as larger animals can fast longer (Bartholomew 1970). For these reasons, sexual size dimorphism is most pronounced in land-breeding seals where the EPP is highest (e.g., elephant and gray seals). While defending estrous females from rival males is not as costly as lactation, males can use their energy stores to sustain a longer fast. This is advantageous for both longer attendance of estrous females as well as for territory defense (Crocker et al. 2012). For example, adult male elephant seals haul out on breeding beaches weeks before the arrival of the first females to establish a dominance hierarchy with rival males and claim the best-pupping sites as territory (Haley et al. 1994). While the lactation interval for each elephant seal mother is only ~26 days, the arrival and departure dates of individual females are staggered across an almost 3-month-long breeding season. The dominant harem master males are larger, which allows them to expend more energy defending the harem as well as prolonging their harem tenure (Deutsch et al. 1990). During this period, they rely solely on their stored energy reserves to sustain them through the entire breeding season losing, 7.8 kg day^{-1} over 89 days, or 39% of their initial mass (Crocker et al. 2012). Interestingly, with relation to male body size, it has been hypothesized that as females are under the greatest energetic constraints, their body size patterns are most optimal and that sexual selection drives male body size relative to that of females (Kienle et al. 2022).

Large body size is less critical and the selective pressures less straightforward for males in species that copulate in the water, as there are advantages and disadvantages to large body size in the maintenance of underwater territories. For these phocids, larger males may have an advantage over smaller males as they would not have to feed as often and would have more time available to compete for and mate with females (e.g., harbor seals; Coltman et al. 1998). However, in species where males maintain territories and copulate in the water, greater fasting ability may not be as important, because males may have access to prey as they patrol their underwater territories, or they might be able to leave on short foraging trips. Moreover, large size may diminish agility when competing for mates underwater. Some of these species even exhibit reverse sexual size dimorphism, where males are smaller than females (e.g., Weddell seals). While little is known about the breeding system of leopard seals, they also exhibit reverse sexual dimorphism, suggesting a breeding system like other aquatically-breeding seals.

8.8 Origins and Evolutionary Implications

It is interesting to consider the origins and selective pressures that shaped the highly derived capital breeding system of phocid seals, as well as when and how it diverged from the ancestral condition. The appearance of key aspects of the life history patterns of phocids, such as increased body size, sexual dimorphism, and diving ability, can be identified in the fossil record (Debey and Pyenson 2013; Cullen et al. 2014; Chap. 1).

The ancestral pinniped, *Enaliarctos* spp., evolved in the North Pacific during the late Oligocene (Berta et al. 1989; Chap. 1). This early pinniped was sexually dimorphic, suggesting that the ancestral state included a polygynous breeding system (Bartholomew 1970; Wyss 1994; Cullen et al. 2014). This small (150–170 cm), fur seal-like primitive carnivore (Churchill et al. 2015) likely made short feeding forays in the coastal ocean when upwelling of cold, nutrient-rich water was greater (Costa and Valenzuela-Toro 2021). Heightened upwelling resulted in greater biological productivity (Lipps and Mitchell 1976), making prey more available. Increased availability of cold ectothermic prey would give endothermic tetrapods an advantage over other predators (Vermeij and Dudley 2000). As a mammal, *Enaliarctos* spp. would have had a high, constant core body temperature which, given a good coat of fur, could be maintained even in cold water. As an air breather, this ancestral seal could maintain an elevated body temperature with a high aerobic metabolism that, in turn, allowed its muscles to perform optimally even when operating in cold water (Costa and Valenzuela-Toro 2021). As upwelled water is cold, the muscles of ectothermic prey are not as efficient, and these organisms would, therefore, be susceptible to predation from faster, more efficient endothermic predators (Cairns et al. 2008; Grady et al. 2019). Thus, the congruence of abundant prey, and the predatory advantage of air-breathing endothermy, likely made it possible for this ancestral seal to invade the coastal marine environment (Costa and Valenzuela-Toro 2021).

Over time, these early pinnipeds diverged into two major lineages: one that refined this coastal intermittent foraging pattern, leading to the otariid and odobenid lifestyles; and a second that increased their diving ability, allowing them to forage farther and deeper offshore, thereby reducing competition with other coastal inshore marine mammals (Costa and Valenzuela-Toro 2021). This second lineage led to the phocid lifestyle. Foraging further away from the colony required an increase in the duration of foraging trips, coupled with a corresponding decrease in the number and frequency of trips, which required a greater energy return per trip. This could be achieved by an increased reliance on stored maternal reserves, allowing a transition from an income to a capital breeding system and, therefore, a separation of feeding from lactation.

As detailed in this chapter, body size is critical to enabling the capital breeding system, and an increase in body size would be consistent with the ability to employ the capital breeding system, as observed in some modern phocid seals. A trend seen in the early evolution of pinnipeds is an initial increase in body size, which first appeared in the early Miocene (23 Ma) as *Allodesmus kelloggi*, a 258-cm Desmatophocid (Mitchell 1975; Barnes 1987) within the 250–350 cm range of northern elephant seal females. Further, seals with large eye orbits tend to be deep divers, and the eye orbits of *Allodesmus* spp. approximate those of modern elephant seals, suggesting that they were also deep divers (Debey and Pyenson 2013). Thus, their large body would not only allow them to dive deep but also enable the separation of feeding from lactation that would have been necessary for utilization of distant offshore foraging grounds, highly dispersed prey, or environments of lower productivity. This life-history pattern would have allowed these early seals to cross the equator and invade the South Pacific Ocean, as well as pass through the region associated with the Central American Seaway and establish breeding populations throughout the Atlantic Ocean (Muizon and Bond 1982; Wyss 1994; Cozzuol 2001; Churchill et al. 2015). Once in the Atlantic, phocids could move north and south as they would have no competition from otariids (see below).

Similarly, phocids would not have been precluded from invading the South Pacific as they could cross the equator (Valenzuela-Toro et al. 2013; Churchill et al. 2014). Large body size and attenuated lactation allowed some species to fully inhabit the predator-free ice and island habitats of the Southern Ocean. As the phocines invaded the Arctic, they became smaller (Chap. 1), most likely in response to the threat of predation (Schulz and Bowen 2004).

It is interesting that, except for elephant seals, there are no modern-day phocids in the temperate to sub-polar regions of the southern hemisphere (Costa et al. 2006) despite the presence of several fossil phocids in these areas (Valenzuela-Toro et al. 2013). It is tempting to speculate that, as income breeders, early otariids would have faced an oceanographic barrier associated with the Central American Seaway (Briscoe et al. 2017). This barrier would cease to exist once the hydrographic conditions changed with the closure of the Central American Seaway around 2.8 Ma (O'Dea et al. 2016). This would have created a migration corridor that allowed otariids to cross and reach the highly productive upwelling regions of the Southern Hemisphere, where they may have outcompeted phocid seals. As otariids have a more energy-intensive lifestyle in highly productive regions, they might have an ability to obtain and invest more resources into reproduction than phocids, who have a more economical lifestyle. This would be consistent with the hypothesis that the reproductive output is greater for species with higher metabolic rates and/or that have a faster pace of life (Hennemann 1983; Schmitz and Lavigne 1984; Dmitriew 2011; Wright et al. 2018). The presence of elephant seals is not surprising as their foraging behavior allows them to utilize resources that are far offshore and very deep, well out of the reach of any otariid.

8.9 Future Directions for Research

Most of the research on phocid reproductive patterns and energetics has been carried out on only a few species of seals, predominately Weddell, elephant, harbor, and gray seals. We have some exciting but limited information on ringed, harp, and hooded seals (Bowen et al. 1985; Lydersen and Hammill 1993; Oftedal et al. 1996; Schulz and Bowen 2004; Ferguson et al. 2018), and we know almost nothing about monk seals and the remaining ice-breeding species such as crabeater, leopard, Ross, ribbon, bearded, Caspian, and Baikal seals. The prolonged lactation interval of Mediterranean monk seals is particularly interesting as it lies significantly outside the range observed for other phocids. The reasons for the lack of data are obvious: as both species of monk seals are endangered, any form of manipulative research is limited, and seals that are found deep in the pack ice or other remote regions require considerable logistical support and are extremely difficult to study. However, research carried out on harp and hooded seals has shown that, given the right resources, even species in challenging environments can be studied (Bowen et al. 1985, 1992; Oftedal et al. 1988, 1996).

We lack fundamental bioenergetics measurements for many species, such as prey assimilation efficiencies and metabolic rates. We also lack data on the birth mass, weaning mass, growth rate, and lactation duration for most phocids. Milk intake measurements and milk composition data have been completed on only a few species, and we have only scratched the surface of the physiological adaptations that allow a phocid pup to process such a vast quantity of lipid-rich milk. A basic understanding of bioenergetics, lactation patterns, and breeding strategies is critical for understanding the mechanistic constraints on behavior and their evolutionary origins. These are also crucial inputs in modeling efforts to predict how environmental disturbance will affect behavior and, ultimately, population dynamics (Costa 2012; McHuron et al. 2017; Pirotta et al. 2018).

While the capital breeding life history pattern typified by some phocids is evolutionarily more derived, the broader distribution of income breeders, as typified by otariids, especially in the southern hemisphere, suggests that when food is more available, the income strategy prevails. Is the phocid life history pattern only advantageous in regions where otariids cannot go? For example, northern and Antarctic fur seals (*Arctocephalus gazella*) overlap with northern and southern elephant seals in the North Pacific and the Southern Ocean, but they forage differently. Fur seals make short, shallow dives in the epipelagic zone, while elephant seals make long, deep dives to the mesopelagic zone (Costa et al. 2010). Further comparisons between different species in different habitats would help elucidate the eco-evolutionary dynamics that drove the emergence of a reproductive strategy as remarkable as the phocid capital breeding system. A better understanding of the energetic constraints faced by species with different reproductive patterns would allow us to predict how they might respond to changing ocean conditions as well as the resilience of these different reproductive patterns to anthropogenic disturbance.

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