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Pinniped Life History

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The term pinniped comes from the Latin *pinna* for "fin" or "feather," and *pedis* for "footed." The taxonomic grouping Pinnipedia is not its own order, but rather is classified within the order Carnivora and consists of three families of marine mammals: Phocidae which are the true seals (i.e., earless seals), Otariidae, the sea lions and fur seals (i.e., eared seals), and Odobenidae, the walrus. Otariids are most easily distinguished by their external ear or pinnae, their large fore-flippers, and the ability to rotate their pelvis on land and walk quadrupedally. Phocids are distinguished by a lack of pinnae, their short, fur covered fore-flippers which have pronounced claws, and their inability to rotate their pelvis to walk quadrupedally on land. Odobenids are easily recognized by their general lack of fur and their pronounced tusks present on both the male and female walrus. Like the Otariids, they can walk quadrupedally on land (see Fig. 1). Taken together there are 33 extant species of pinnipeds which can be found in almost all marine waters of the globe, though distribution patterns can be seen between groups. Only phocids are founds in the Arctic and Antarctic with the exception of the walrus (found in northern circumpolar waters). Most fur seal populations are restricted to the southern hemisphere, yet most other otarriids are found in both hemispheres. The Hawaiian (*Monachus schauinslandi*) and Mediterranean monk seals (*Monachus monachus*) are the only tropic species, and the Baikal seal (*Pusa sibirica*) is the only freshwater species. While pinnipeds inhabit all climate zones, they are not currently in the waters off the coast of Asia or India, and it is suggested that these waters are nutrient poor and therefore do not have a stable food supply for them (Riedman 1990).

Evolution

Pinnipeds are thought to have evolved from their terrestrial ancestors, a group termed the Canoidea. Since Canoidea consists of multiple groups such as the ursids (bears), mustelids (weasels and otters), and canids (dogs), there has historically been argument within the scientific community as to the specific phylogenetic origins of the three pinniped families (Arnason et al. 2006; Lowenstein 1986; for a recent in-depth review of the debate see Koretsky et al. 2016). There are two views of their ancestry centered around the question of whether pinnipeds evolved from the same, or two different, phylogenetic lines. The diphyletic view states that both otariids and odobenids evolved from a bear-like ancestor around 25

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Pinniped Life History, Fig. 1 Photographs of three-species representative of the three pinniped families: (**a**) Family Phocidae, *Phoca vitulina* (harbor seal); (**b**) Family Otariidae, *Zalophus californianus* (California sea lion); (**c**) Family Odobenidae, *Odobenus rosmarus* (walrus) (Photo credits: Candyce Paparo, Long Island Aquarium & Exhibition Center/Center for the Study of Pinniped Ecology & Cognition (**a**, **b**); Center for the Study of Pinniped Ecology & Cognition (**c**))

million years ago (MYA) in the early Miocene while the phocids evolved from a mustelid or otter-like ancestor about 20 MYA, mid-Miocene (Koretsky and Holec 2002; Koretsky and Sanders 2002; Koretsky and Barnes 2003; Repenning 1976; Riedman 1990). While this view has been supported by the fossil record, recent molecular evidence (e.g., DNA and RNA from extant species) suggests a monophyletic view with phocids and otariids descending from a common bear-like ancestor approximately 25 MYA (early Miocene) (Arnason et al. 2006; Dasmahapatra et al. 2009; Higdon et al. 2007, 2008) Despite conflicting evidence between the fossil record and molecular data, the current scientific consensus is the monophyletic view emphasizing a common ancestor; however, there is still some debate as to whether their most recent common terrestrial ancestors are ursids (bears) or mustelids (weasels/otters) (Berta and Churchill 2012; Boness and Bowen 1996).

Currently, of the 33-extant species of pinnipeds, four phocids and one otariid are listed as endangered with five phocid and two otariids listed as threatened (United States Fish and Wildlife (USFW) 2017). The Caribbean (or West Indian) monk seal (*neomonachus tropicalis*) was listed as threatened on March 11, 1967, and officially declared extinct as of October 28, 2008, being removed from the Federal Register after there had been no reported sightings of the seal in 50 years (USFW 2016). The Hawaiian monk seal (*Monachus schauinslandi*) was listed as endangered as of June 2, 1970 (USFW 2017), and critically endangered in 2008 (Karamanlidis and Dendrinos 2015; Littnan et al. 2015) with the recent population estimates at 1,112 individuals (National Oceanic and Atmospheric Administration (NOAA) 2015). While many pinniped populations are thriving, the factors influencing the 12 species listed as threatened or endangered is the focus of many research and conservation efforts. Data show that the species' populations most in danger are those that inhabit the subtropical/tropical and Arctic/Antarctic regions of the globe (i.e., the more northern and southern latitudes), with more temperate dwelling species having stable and even thriving populations (Ferguson and Higdon 2006). This suggests that the more extreme areas of the globe may be more susceptible to both natural and man-made changes in the ecosystem. The underlying causes of this relationship between latitude and population stability is an area of research with investigations focused on the interactions between ecology and the life history of these varied pinniped species with an emphasis on climate change and prey distribution/availability (Ferguson and Higdon 2006).

The life history of pinnipeds is especially multidimensional because they are amphibious marine mammals that carry out critical life functions both on land and in the water. Their evolutionary ties to their terrestrial ancestors are demonstrated by their dependence on the sea for foraging while often breeding and giving birth on land. While the challenges of individual species vary, there are several generalizations that can be made within the life history of pinnipeds as a group with major differences being drawn between the phylogenetic lines of the phocids and otarioids (both the otariids and odobenids).

Life Span

The life span of pinniped species ranges from 15 to 30 years with males having a shorter span due to the added biological stressors and potential injuries incurred during male-male aggressive encounters (see Table 1). It has been shown that many northern elephant seals (*Mirounga angustirostris*) die before reaching sexually maturity (age five) and significantly more die before reaching age nine at which time they are considered able to successfully compete for females and reproduce (Le Boeuf 1981; Reiter et al. 1981).

As mentioned above, it should be noted that chronological age of reproductive maturity (age at which they are physically capable of breeding) is different than the age at which an animal successfully breeds. Typically, females breed once they hit sexually maturity (e.g., age two), but they may not give birth for a few more years (e.g., 4–5 years of age) (Boness et al. 2002; Riedman 1990). This discrepancy in age is more pronounced in male pinnipeds, perhaps because they must be physically capable of breeding, as well as physically large enough and behaviorally mature enough, to compete for territory/females. For example, walrus (*Odobenus rosmarus*) reach sexual maturity at 9–10 years of age but may not breed successfully until 13–16 years old (Fay 1982).

Reproduction

Overall, both male and female pinnipeds must have sufficient mass and a healthy body condition, as well as the behavioral maturity, to breed successfully and reproduce. Sexually mature pinnipeds typically come ashore to their natal beaches (the site at which they were born) each year to give birth and then mate (Hoffman and Forcada 2012). Most otariids breed and give birth on land (Boness 1991; Franco-Trecu et al. 2015; Giardino et al. 2016), while 15 of the 18 phocid species mate aquatically (for an extensive review of aquatic breeding phocids see Van Parijs 2003). Most exceptions seem to be the ice seals, though data exist for a limited number of species. For example, evidence suggests that weddell seals (*Leptonychotes weddellii*) do not return to breed at the site where they were born (Davis et al. 2008), and they are the only large phocid to breed exclusively on fast-ice (i.e., ice attached to land). This may be due to female movement being restricted to consistent breathing holes in the ice (Cline et al. 1971; Bartsch et al. 1992; Harcourt et al. 1998, 2000).

As amphibious marine mammals, access to land for mating and/or birthing is critical and therefore timing of the annual breeding/pupping season is important. Female estrous cycles (when females are physiologically receptive for breeding) are annually synchronous for all pinnipeds, and mating occurs relatively quickly after the birthing or parturition process. Though this timeframe between birthing and mating ranges somewhat among species, pinnipeds manage to synchronize in part through embryonic diapause or delayed implantation (Pomeroy 2011). In this way, the egg is fertilized and develops for approximately 7–10 days at which point development pauses at the blastocyst stage. Up to several months later (timing depending on the species), the embryo begins to develop again and implants into the uterus. This delay allows for the gestation period (including the diapause) to last approximately 10–12 months, ensuring that sexually mature males and receptive females arrive at their breeding sites at the same time each year.

Females give birth to one offspring per year of sexual maturity, though this is in part dependent on environmental factors such as food supply. Females may not give birth in a certain year if there are not enough resources available and her body is not in a healthy condition to sustain a pregnancy and lactation period (Boyd 2000; Shero et al. 2015). Twinning is rare, though has been documented (Hoffman and Forcada 2009; Riedman 1990), but research suggests that having twins may be detrimental as it decreases overall

Pinniped Life History, Table 1 Information on 26 of the 33 extant species of pinnipeds. The data provide descriptions of general aspects of life history, organized by taxonomic family, including average mass of males and females of a species, existence of sexual dimorphism, life span, breeding strategy, lactation length, and percent milkfat. These data allow one to compare not only across species but across and within the phocid, otariid, and odobenid families. There is not sufficient data reported to provide a valid average of milkfat when "nd" is indicated in the table

Common name *Scientific name*	Ave female mass	Ave male mass	Sexual dimorphism	Life span (yrs)	Breeding strategy	Ave lactation length	Ave % milkfat	Source[a]
Phocidae								
Baikal seal	130 kg	130 kg	No	50–55	Monogamy	2 months	nd	1, 2, 3
Pusa sibirica								
Bearded seal	260–360 kg	260–360 kg	Slight; females larger	25	Monogamy/Slight polygyny	2–3 weeks	49	4, 5, 6
Erignathus barbatus								
Grey seal	250 kg	400 kg	Yes	25–35	Moderate polygyny/ Ice breeders monogamous	2–3 weeks	60	7, 8, 9, 6
Halichoerus grypus								
Harbor seal	110 kg	110 kg	No	25–30	Slight polygyny	3–4 weeks	50	6, 9
Phoca vitulina								
Harp seal	135 kg	135 kg	No	Unknown	Slight polygyny	12 days	57	6, 10, 11, 12
Pagophilus groenlandicus								
Hawaiian monk seal	170–205 kg	170–205 kg	Slight; females larger	25–30	Slight polygyny	4–6 weeks	nd	3, 6, 13
Monachus schauinslandi								
Hooded seal	200 kg	300 kg	Yes	30–35	Slight polygyny	3–5 days	61	6, 14, 15

Cystophora cristata								
Mediterranean monk seal	240–400 kg	240–400 kg	Slight; males larger	20–25	Slight polygyny	4 months	nd	3, 6, 16, 17
Monachus monachus								
Northern elephant seal	600 kg	2000 kg	Yes	13–19	Extreme polygyny	3–4 weeks	54	6, 18, 19
Mirounga angustirostris								
Phocidae								
Ribbon seal	80 kg	80 kg	No	20–30	Slight polygyny	3–5 weeks	nd	3, 6, 20
Histriophoca fasciata								
Ringed seal	50–70 kg; 110 kq for Saimaa subspecies	50–70 kg; 110 kg for Saimaa subspecies	No	25–30	Monogamy/Slight polygyny	6 weeks	42	6, 21, 22, 23
Phoca hispida								
Southern elephant seal	400–900 kg	1–2 tonnes	Yes	10–20	Extreme polygamy	3 weeks	40	3, 24, 25
Mirounga leonina								
Spotted seal	65–115 kg	65–115 kg	No	30–35	Monogamy/Slight polygyny	5–6 weeks	nd	6, 26
Phoca largha								
Weddell seal	1200 lbs. (544 kg)	544 kg	No	20–30	Slight/Moderate polygyny	7 weeks	48	6, 27
Leptonychotes weddellii								
Otariidae								
Antarctic fur seal	22–50 kg	130–200 kg	Yes	15–25	Moderate polygyny	4 months	42	3, 28, 29, 30

(*continued*)

Pinniped Life History, Table 1 (continued)

Common name *Scientific name*	Ave female mass	Ave male mass	Sexual dimorphism	Life span (yrs)	Breeding strategy	Ave lactation length	Ave % milkfat	Source[a]
Arctocephalus gazella								
Australian sea lion	61–105 kg	180–250 kg	Yes	20–25	Moderate polygyny	11–12 months	nd	3, 31, 32, 33
Neophoca cinerea								
California Sea Lion	110 kg	315 kg	Yes	20–30	Moderate polygyny	10 months	44	3, 6, 34
Zalophus californianus								
Galapogos fur seal	27–28 kg	60–68 kg	Yes	20–25	Moderate polygyny	18 months	29	35, 36
Arctocephalus galapagoensis								
Otariidae								
Guadalupe fur seal	40–50 kg	160–180 kg	Yes	20	Moderate polygyny	9 months	nd	6, 37
Arctocephalus townsendi								
New Zealand sea lion	90–165 kg	300–450 kg	Yes	~20	Extreme polygyny	12 months	nd	3, 38, 32
Phocarctos hookeri								
Northern fur seal	60 kg	270 kg	Yes	10–27	Extreme polygyny	4–5 months	42	6, 39, 40

Callorhinus ursinus								
Southern sea lion	170 kg	300–350 kg	Yes	15–20	Moderate polygyny	11–12 months	47	3, 41, 42, 43
Otaria byronia								
Steller sea lion	350 kg	1120 kg	Yes	20–30	Extreme polygyny	11–12 months	24	3, 6, 44
Eumetopias jubatus								
Subantarctic fur seal	25–67 kg	70–165 kg	Yes	15–20	Moderate polygyny	11 months	42	3, 45, 46
Arctocephalus tropicalis								
Odobenidae								
Walrus	580–1039 kg	880–1557 kg	Yes	30–40	Polygyny	2–3 years	30	5, 6, 47, 48
Odobenus rosmarus								

[a]1, Nomokonova et al. 2013; 2, Pastukhov 1990; 3, Riedman 1990; 4, Burns 1981a; 5, Fay 1982; 6, NOAA 2016; 7, Amoroso et al. 1950; 8, Boness and James 1979; 9, Fedak and Anderson 1982; 10, Bowen and Sergeant 1983; 11, Kovacs and Lavigne 1986; 12, Oftedal et al. 1993; 13, Alcorn and Buelna 1989; 14, Bowen et al. 1985; 15, Kovacs and Lavigne 1992; 16, Aguilar et al. 2007; 17, Pomeroy 2011; 18, Crocker et al. 2001; 19, Reiter et al. 1978; 20, Burns 1981b; 21, McLaren 1958; 22, Hammill et al. 1991; 23, Zhang et al. 2014; 24, Carrick et al. 1962; 25, Hofmeyr 2015a; 26, Boveng 2016; 27, Kaufman et al. 1975; 28, Payne 1979; 29, Kerley 1985; 30, Doidge et al. 1986; 31, Goldsworthy 2015; 32, Marlow 1975; 33, Ling and Walker 1976; 34, Stewarts and Yochem 1984; 35, Trillmich 1979; 36, Trillmich and Lechner 1986; 37, Gallo-Reynoso and Figueroa-Carranza 1996; 38, Chivers 2015; 39, Peterson 1965; 40, Costa and Gentry 1986; 41, Cárdenas-Alayza et al. 2016; 42, Hamilton 1934; 43, Vaz-Ferreira and Ponce de Leon 1987; 44, Costa 1991; 45, Hofmeyr 2015b; 46, Roux and Hess 1984; 47, Kastelein et al. 2014; 48, Lowry 2016

survival rates (Schultz et al. 2011). Alloparenting, a system in which individuals in the population other than the mother contribute to the care of the offspring, is rare but has been observed in the pinnipeds (Boness and Bowen 1996; Porter and Trites 2004; Schulz and Bowen 2005). It is most likely to occur when a female has lost her pup and fosters one that has lost its mother. Rarely, females will nurse a stray pup alongside its own. Males do not offer paternal care and, as stated, females do not usually care for offspring that are not their own. In fact, females have been known to behave aggressively toward nonfilial pups attempting to nurse. Infanticide has been observed but is usually caused by a nonfilial pup continuing to approach and attempt to nurse from an aggressive female, or by incidental injury due to proximity of an aggressive male-male interaction, though males have been known to kill pups through directed aggressive contact (Kiyota and Okamura 2005).

Breeding Strategies

The details of mating strategies vary between species but most are polygynous and fall under either of two categories: harem or lek breeding systems (for a more detailed review see also Boness et al. 2002). In a harem system, the males fight for dominance rankings and access to receptive females on the beach. The most dominant male will spend the breeding season alternating between mating with many females and fighting off male challengers. Due to the physical nature of the male-male competition, many do not mate successfully until they are approximately 10 years old, even though sexual maturity may have been reached at 4 years of age (see "Life Span"). Males must acquire the size and the experience to win fights with the older, more dominant, males each year to gain access to females. For example, male northern elephant seals herd females inside their territory and keep other males out while male California sea lions (*Zalophus californianus*) compete to control specific locations on the beach. Unlike elephant seals, the female sea lions are free to move between these areas and therefore from male to male. Conversely, male harbor seals (*Phoca vitulina*) demonstrate a lek system and do not tend to have physical altercations with each other during the breeding season, but rather vocalize underwater to claim a territory therefore advertising their presence to females and deterring other males from that area (Van Parijs 2003). This difference in breeding style may be related to resource availability (food and breathing holes for ice seals), mating location (females of species that mate aquatically have more control over their mate choice), and the extent of sexual dimorphism (difference in physical size between males and females) found between various species (Van Paris 2003; González-Suárez and Cassini 2014; Modig 1996). Elephant seals have the largest degree of sexual dimorphism with the female northern elephant seals being an average of 1,300 pounds (600 kg) and males three to five times that at an average of 4,400 pounds (2,000 kg) (see Table 1). Their breeding strategy consisting of males fighting, often violently, to attain dominance and control of females favors the evolution of a large body size. Harbor seals, on the other hand, demonstrate little to no sexual dimorphism, with males and females both averaging 245 pounds (110 kg), and they demonstrate little to no male-male aggression during the breeding season.

Reproductive success rates are based on number of offspring produced throughout the life span. While this is well defined and relatively easy to quantify for females of a given species, the data is less discernable for males. Regardless of the breeding strategy employed by a species, females give birth to one offspring per year (as noted, twins are rare and most due not survive to maturity), but males mate with multiple females each season making DNA testing the most reliable way to determine paternity and male success rate in a population. Due to the inherent difficulty of DNA testing for male success rates each year, most estimates are based on observed successful copulations and known dominance ranking of individual males. While this seems a reasonable assessment of male success, some data indicate that the most dominant males may not necessarily be providing the DNA for all offspring. For example, in northern elephant seals, "sneaker" males (young juveniles that "sneak" a copulation with a female) have been found to have contributed DNA to the population despite their lower dominance ranking and smaller size (de Bruyn et al. 2011). They have been successful in mating with females on the outer edges of a harem while the dominant male is engaged in a copulation, a fight with another male, or sleeping (hence the term sneaker male). This is interesting to note in relation to the evolution of behavioral/cognitive strategies in pinniped species.

Maternal Dependency/Lactation

Care of offspring in pinnipeds centers around females and consists of protection from predators but primarily lactation or milk production. The mother-pup bond is strong during the lactation period and decreases significantly, and perhaps completely, after weaning. However, there is evidence that females behave in an affiliative manner with their kin when returning to their natal beaches to breed each year (Insley et al. 2003; Schusterman et al. 2002), and there is some evidence that a California sea lion and its mother recognized each other for many years (Hanggi and Schusterman 1990).

Length of maternal dependence and lactation is generally divided between pinniped families, though it should be noted that other factors such as body size, ecology, foraging strategy, breeding/birthing location, and substrate all play an integrated role in the lactation strategy displayed by a given species (Bartholomew 1970). The phocids have the shortest lactation period ranging from four days (hooded seal, *Cystophora cristata*) to two and one half months (Baikal seal, *Pusa sibirica*; Pastukhov 1993), with a milk containing 40–50% fat (see Table 1). Otariids have a moderate nursing period between 4 months and 3 years with approximately 20–35% milkfat, while odobenids average a 2–3 year lactation period with about 30% milkfat, making them the pinniped with the longest period of maternal care (see Table 1). In fact, the walrus is the only species to have adopted a strategy of nursing their young in the water and having their young accompany them on foraging trips (Schulz and Bowen 2005). Therefore, three predominant lactation strategies (discussed below) can be seen among female pinnipeds which are generally divided among phylogenetic lines (and will be discussed as such for purposes of generalizing here), though the interactions between species ancestry, maternal mass, breeding substrate, thermoregulation challenges, milk composition, and various other ecological factors must not be overlooked (for a detailed review see Schulz and Bowen 2005).

A *fasting strategy* with little to no feeding is employed by phocids, though the harbor seal and ringed seal (*Phoca hispida*) have been documented to occasionally forage during this time. This may be correlated with their smaller body size, creating an inability to maintain enough energy reserves of their own throughout lactation (Boness and Bowen 1996; Bowden et al. 1992). This foraging during lactation may also be related to the availability of food close to shore, which may entice them to feed later in the lactation period (Boyd 1998). Length of lactation period is correlated with maternal mass and percent of milk fat. The shorter the lactation period (for all pinnipeds), the more quickly fat reserves must be transferred to pups in the form of milk. Therefore, larger females can handle dumping more fat rich milk into their pups quickly. Of course, longer lactation periods mean more maternal care/time for pup growth and protection from predators; however, if fasting, there will always be an upper limit by which the female must return to sea or risk decreasing her reserves to the point by which she can no longer survive.

Ice-breeding phocids fast and have the shortest lactation periods of all pinnipeds, an advantage in an environment where a mother and pup are together on either fast (attached) or pack (floating) ice. For example, if the ice were to crack, break, and/or float away, a foraging female may not be able to find her pup upon returning to the ice. Breaking ice could crush or drown a pup. Also, in an extremely cold climate, adding blubber to a pup as quickly as possible will help it to thermoregulate appropriately.

Otariids have adopted a *foraging-cycle strategy* meaning that they alternate, or cycle, between nursing and foraging throughout the lactation period. This allows for a longer duration of maternal care, as the females replenish their energy reserves between nursing bouts. Whether this strategy is advantageous because it allows them to care for their pups for longer periods of time while not overly depleting their own reserves, or if it is more energetically demanding in the long run, is an area of continued study (Coltman et al. 1997; see Schulz and Bowen 2005). Perhaps the otariids, being small bodied as compared to most phocids, simply cannot acquire the energy reserves needed for fasting while lactating. These foraging bouts also add another challenge for these mother-pup pairs, as the pups are left alone in the rookery while the mother goes to sea to forage for 2–3 days. When the female returns after a foraging trip of 1–6 days, she and her pup must overcome the challenge of reuniting among hundreds of other mother-pup pairs (see Insley 2000; Trimble and Insley 2010).

A third strategy, the *aquatic nursing strategy*, is only found in the odobenids. The walrus, having the longest period of maternal care (2–3 years), has adopted a strategy of nursing in the water, as opposed to exclusively on land, and pups are known to accompany their mothers on foraging trips (Boness and Bowen 1996; Fay 1982). Walrus pups are born the least precocious of the pinnipeds, and this lengthy dependence on the mother allows for a longer maturation process of the pup prior to survival on its own.

Foraging

The majority of a pinniped's fresh water supply is extracted from the food they eat and some is acquired through the metabolism of their blubber layer. Pinnipeds have been known to consume salt water in small amounts and metabolize it ending with a freshwater gain, but the process requires a lot of energy and is not an efficient source of hydration (Riedman 1990).

Pinnipeds tend to be generalists with diets consisting primarily of fish, crustaceans, and cephalopods and are typically solitary hunters though they have been documented hunting cooperatively when herding a large school of fish (Gales et al. 2004; Riedman 1990). A few species are specialists and as such have adaptations for feeding on certain prey items. For example, the crabeater seal (*Lobodon carcinophagus*) eats krill, and its teeth are formed in a way that allows them to gulp water and strain it out leaving the krill in their mouths on which to feed. Bearded seals (*Erignathus barbatus*) and walrus feed on mollusks and other bottom dwelling invertebrates. They both have substantial vibrissae, or whiskers, with which they use for rooting through muddy substrates and the walrus' mouth can produce suction strong enough to pull mollusks out of their shells. Ringed seals feed primarily on crustaceans and elephant seals prefer squid. The leopard seal (*Hydrurga leptonyx*), found in Antarctica, eats penguins and is the only pinniped known to prey on other seals (typically young crabeater seals) (Hocking et al. 2013).

Foraging occurs at varying depths and durations based on species, but a notable mention with significant diving abilities is the elephant seal, known to make foraging dives to an average depth of 1,680 feet (512 m) and 22 min in length (Heerah et al. 2014). The elephant seals' maximum recorded dive depth is 6,562 feet (2,000 m) and for a duration of approximately two hours, rivalling that of the sperm whale, making it one of the deepest diving marine mammals. These long dives are in part possible due to their large size which increases the amount of oxygen they can store and therefore increasing time spent at depth and decreasing the need to come up for air frequently.

As amphibious mammals, pinnipeds must balance the energetic resources needed to leave a terrestrial haul-out location and actively search and hunt for food with the energy gained by the food they consume. Foraging patterns are correlated with, and generally divided by, ancestry with the phocids most likely to employ an *income strategy* and otarioids using a *capital strategy* (Arthur et al. 2016; Stephens et al. 2014). For example, the hooded seal (a phocid) tends to favor a capital strategy based on fewer trips with longer travel distances to and from foraging sites of large density prey (through which they increase reserves in body mass – creating capital reserves), while the California sea lion (an otariid) favors an income strategy with shorter, but more frequent, foraging trips (less reserve and more frequent income replenishment needed). The quality of prey is also important as traveling a long distance for many poor-quality fish will not be energetically advantageous over traveling a shorter distance for fewer fish, if the smaller fish population is a much higher quality. Latitude ranges will, in part, determine prey distribution with colder/temperate waters, and therefore middle latitudes, having higher productivity and prey item availability.

Therefore, factors correlated with a capital versus income foraging strategies (and with the phocid and otarioid groups, respectively) are the species' overall body size, maternal care/lactation strategy (see "Reproduction"), and global distribution. Whether the driving factors of strategy are ancestry, physical properties of the species (e.g., overall size and depth of blubber layer), water temperature and quality, or habitat ecology including prey availability/distribution is an active area of research. These factors are inherently interconnected and it is probable that rather than a direct causal link, the best predictor of foraging strategy will be an interactive model of the aforementioned variables.

Molting

Molting is another event tethering these amphibious marine mammals to land. All species molt, during which time they undergo a relatively drastic shedding of their fur accompanied by the growth of a new coat. The timing of the molt depends on the species as well as the age within species. For example, molting is staggered by age in the northern elephant seal with yearlings hauling out in the fall, adult females in the spring after foraging trips following the breeding season, and adult males molting in the summer (Longstreth 2016; Riedman 1990). Pups of all species go through an initial molt of their lanugo, which is a layer of fur that develops in utero and serves to help newborn pups maintain their core body temperature until their blubber reserves have increased. Some pups (e.g., the harbor seal) shed their lanugo in utero (prior to birth), but most pinnipeds shed it by the end of weaning (Bruemmer 1975; Riedman 1990).

While many terrestrial mammals are known to shed throughout the year with marked changes in this based on seasonality/temperature, the pinniped molt is notably different in large part due to their semiaquatic lifestyle. The growth of new fur requires increased blood flow to the surface of the skin. This is counter to the needs of marine mammals in that they often shunt blood away from the surface to their core (major organs and large muscles) to limit heat loss to the aquatic environment (Erdsack et al. 2012). Therefore, growing new fur and maintaining their core body temperature are essentially at odds. Many pinnipeds compensate for this by not shedding and growing hair continuously throughout the year, but rather by condensing this process into a yearly event or molt. During this time, they remain on land for relatively long periods of time allowing the blood to remain at the surface of the skin providing the nutrients needed for new hair growth.

Among the pinnipeds two main molting strategies emerge: one being to increase body mass (foraging), then fast and remain out of the water (more blood supply to the skin/new fur) allowing for a short molt duration, while the second is to continue to forage throughout the molt, entering the water (interrupted blood supply to the skin/new fur), thus requiring a longer molt duration. Which strategy is employed can be generalized as a division between the phocid and otarioid lines. Harbor seals (a phocid) have relatively short molts lasting on average 1 month while the molt of a California sea lion (an otariid) can last up to a few months with a peak in shedding lasting a month or more. However, it must be noted that there are many interacting variables underlying reliance on these strategies other than ancestry (see "Foraging").

An extreme strategy in the phocid line is employed by elephant seal species and the Hawaiian monk seal. They haul out once per year and not only shed their fur but their skin as well. Large patches of their hair and skin peel off to reveal new skin and fur below. This process has been term a *catastrophic molt* and requires a lot of energy and a large blood supply to the surface of the body (Ling 1970). Therefore, these seals fall under the category of a short duration molt during which time they fast and remain on the beach until its completion.

Migrations

Pinnipeds have a consistent and annual migratory pattern primarily based on feeding, breeding/birthing, molting, and seasonal ice (for the Arctic/Antarctic species) (see Luschi 2013). They migrate to breed and give birth, traveling to warmer waters for the new pups that lack a thick blubber layer for thermoregulation and then to cooler waters with greater productivity and more prey items. An exception to this are many of the ice seals as they prefer to breed when the ice is most prevalent allowing for larger areas for breeding and pupping and a lowered chance of fast ice breaking off and becoming a moving ice floe. If this were to happen during the weaning period, females could be separated from their pup (see "Reproduction").

The methods by which pinnipeds navigate during these migrations are not completely understood. Researchers believe that it is a combination of their ability to use underwater landmarks, water and wind currents, water temperature, and even celestial bodies. Mauck et al. (2008) found that the harbor seal can utilize the stars in the night sky to navigate, and Ronald and Healey (1981) found that juvenile harp seals (*Pagophilus groenlandicus*) are successful on their annual northern migration (up to about 3,100 miles/5,000 km) on their first trip with no adult seal present. This indicates that, at least in some cases, aspects of these migrations may be innate.

Conclusion

The life history of a species encompasses a pattern of resource acquisition and utilization in support of the interactions between lifespan, foraging, and reproduction strategies (which may or may not include migratory patterns in relation to prey and/or mate availability and access). This interrelated web of factors is based on the evolutionary history of a species, the past and present environmental pressures, and the ecological systems in place. The above sections are an overview of the basic points of life history within the pinnipeds but, as with any taxonomic group, the physiological and behavioral aspects of these animals are not only influenced by the past and current environments but will continue to be shaped by their environments to come.

Cross-References

- ▶ Pinniped Cognition
- ▶ Pinniped Communication
- ▶ Pinniped Diet
- ▶ Pinniped Locomotion
- ▶ Pinniped Morphology
- ▶ Pinniped Navigation
- ▶ Pinniped Sensory Systems

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