

Chapter 10

Northern Elephant Seal (*Mirounga angustirostris*, Gill 1866)



María C. García-Aguilar

Abstract The northern elephant seal (*Mirounga angustirostris*) is the largest carnivore in the Northern Hemisphere. They are sexually dimorphic with adult males weighing up to 2000 kg and measuring up to 4.5 m and adult females weighing up to 700 kg and measuring up to 3 m. In addition to the differences in weight and length, adult males have a facial proboscis, which gives the common name “elephant.” It is a deep-diving marine mammal that can dive to depths over 1500 m. The species forages within the cold waters of the North Pacific Ocean. Breeding sites are located mainly on sandy beaches of temperate islands and a few mainland coastal areas of California, USA, and Baja California, Mexico. Despite being nearly driven to extinction due to the intense commercial harvesting in the nineteenth century, the northern elephant seal has recolonized its historical range and as of 2010 had an estimated population size of 201,000 individuals. However, due to low genetic diversity, a consequence of the population bottleneck, the main threats to the species appear to be disease outbreaks and environmental changes.

Keywords Phocids · Northeastern Pacific Ocean · Deep diving · Sexual dimorphism

General Features

The northern elephant seal (*Mirounga angustirostris*) is a member of the family Phocidae (“true seals”), subfamily Monachinae (“southern seals”), which includes three groups: Lobodontini, *Mirounga*, and *Monachus* (Fyler et al. 2005). While the North Atlantic origin of Monachinae seals is widely accepted, the origin of *Mirounga* is not clear due to the lack of fossil record (Deméré et al. 2003; Fyler et al. 2005). The known phylogenetic history of *Mirounga* begins with *Callophoca*, a lineage

M. C. García-Aguilar (✉)

Departamento de Oceanología Biológica, Centro de Investigación Científica y de Educación Superior de Ensenada, Ensenada, Baja California, Mexico
e-mail: gaguilar@cicese.mx

© Springer Nature Switzerland AG 2021

G. Heckel, Y. Schramm (eds.), *Ecology and Conservation of Pinnipeds in Latin America*, https://doi.org/10.1007/978-3-030-63177-2_10

191

that may have evolved in the eastern North Atlantic, more than 4.5 Ma, and dispersed westward through the North Equatorial Current to the coasts of North America (Ray 1976; de Muizon 1982). Some members of this lineage could have traveled in the late Miocene or early Pliocene through the Central American Seaway, open at those times, and settled in the eastern South Pacific (Deméré et al. 2003). Speciation resulted in the southern species (*M. leonina*), while the northern species (*M. angustirostris*) could have resulted from a transequatorial event and allopatric speciation, possibly during the Pleistocene (Deméré et al. 2003). Currently, the southern elephant seal is distributed in the Southern Ocean and the northern elephant seal in the Northeastern Pacific Ocean (Hindell and Perrin 2008).

Northern elephant seals are extremely sexually dimorphic in adulthood (Fig. 10.1) with males weighing as much as 2000 kg and measuring up to 4.5 m in length while females weigh between 400 and 700 kg and measure about 3 m in length (Deutsch et al. 1990, 1994). At birth there are no weight and length differences between the sexes, but when weaned, males are slightly heavier (4%) and longer (1%) than females (Salogni et al. 2018). Along with the difference in body size, adult males develop a fleshy proboscis on their head and have a wide hairless neck and a reddish dermal shield on the chest (Le Boeuf and Laws 1994). In both sexes, the pelage is short and rough and replaced to the epidermis once a year when they haul out to molt (Le Boeuf and Laws 1994). Pelage in adult males is dark brown, and in females, it is light brown. Pups are born black and then molt between the fifth and sixth week



Fig. 10.1 Northern elephant seal male and group of adult females with pups. (Photo: M.C. García-Aguilar)



Fig. 10.2 Group of weaned pups showing pelage of molted and unmolted pup. (Photo: M.C. García-Aguilar)

to a silvery color (Fig. 10.2) (Le Boeuf and Laws 1994). Northern elephant seals have vibrissae on their snout and above their large, round, and black eyes. The hind flippers are emarginated and hairy and lack nails. The adult dentition is $i\ 2/1$, $c\ 1/1$, $pc\ 5/5$, total 30, and the canines are sexually dimorphic in size and shape (Stewart and Huber 1993).

Females can live up to 21 years, while males live up to 15 years (Condit et al. 2013). The age of first reproduction for females ranges from 3 to 8 years, with an average of 3–4 years (Reiter et al. 1981; Sydeman et al. 1991; Sydeman and Nur 1994). The age of first reproduction for males varies between 5 and 10 years (average 8 years), being more successful breeders after 12 years of age (Clinton and Le Boeuf 1993).

Northern elephant seals are physiologically adapted to cold water, but heat dissipation can be a problem when they are on land. Elephant seals do not pant or sweat, and heat is dissipated through thermal windows (Khamas et al. 2012; Codde et al. 2016), which are body surfaces that function as a temporary heat dissipater under conditions of thermal stress (Mauck et al. 2003). Locomotion on land is energetically very expensive given their enormous body size and the fact that they do not use the hind flippers to move (Tennett et al. 2018). Their haul-out period has four phases (Fig. 10.3): (1) the winter breeding season, (2) the spring molt of adult females and juveniles (i.e., sexually immature individuals of both sexes), (3) the summer molt of subadult and adult males, and (4) the autumn haul-out of juveniles (Le Boeuf and Laws 1994). The preferred sites to breed, molt, and haul out are soft sloping sandy beaches, but they are sometimes found on rocky substrates.

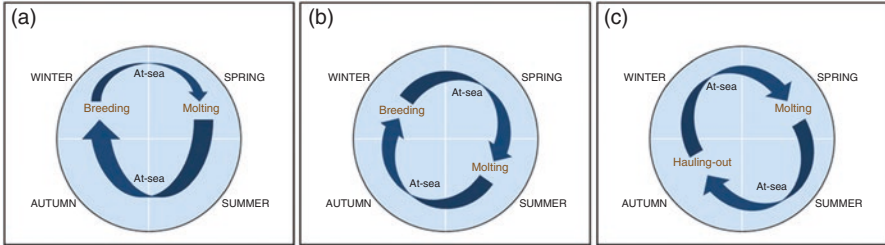


Fig. 10.3 The annual cycle of northern elephant seals. (a) Adult females, (b) subadult and adult males, and (c) juveniles

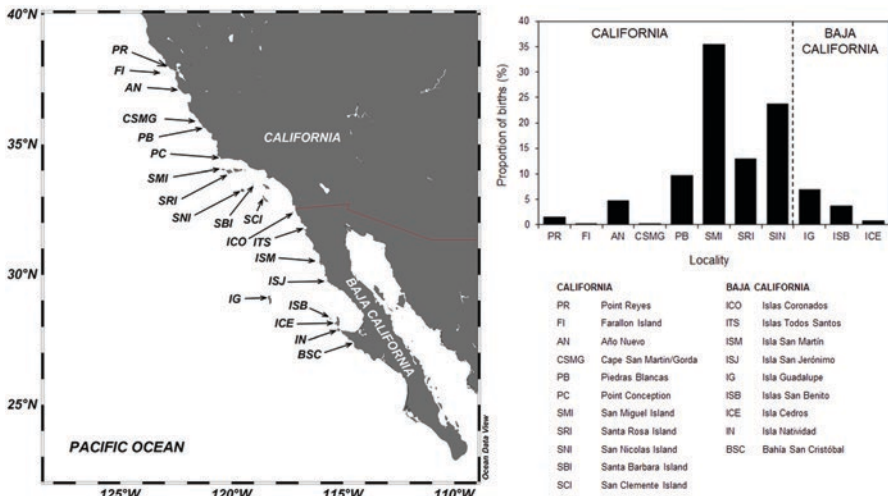


Fig. 10.4 Breeding and haul-out sites in California, USA, and Baja California, Mexico, with 2009–2010 proportion (%) of births in the main colonies. Based on Lowry et al. (2014) and García-Aguilar et al. (2018)

Distribution and Abundance

Archaeological evidence shows that northern elephant seals were established in southern California 15,000 years ago and that they were an important resource for Native Americans (Le Boeuf and Laws 1994). Their breeding and haul-out sites are located mainly on islands of California, USA, and Baja California, Mexico, with some isolated continental mainland locations of the California coast (Le Boeuf and Laws 1994; Lowry et al. 2014) (Fig. 10.4).

The northern elephant seal was subjected to intense commercial harvest during the nineteenth century. Population size and distribution before hunting are unknown, but it is presumed that they were distributed from central California to Bahía San Cristóbal, in Baja California Sur, Mexico (Fig. 10.4). Scammon (1870) noted that

elephant seals were scarce in the 1850s and were considered extinct by the end of the 1870s (Townsend 1885). Nevertheless, in the early 1880s, some elephant seals were found at Bahía San Cristobal and at Isla Guadalupe, Baja California; those animals were killed, and in 1884 the species was again declared as being extinct (Le Boeuf and Laws 1994). A few years later, in 1892, nine individuals were discovered at Isla Guadalupe, seven of which were killed for the Smithsonian Museum's collection, and again elephant seals were considered extinct (Le Boeuf and Laws 1994). At the beginning of the twentieth century, expeditions to Isla Guadalupe continued to hunt elephant seals. In 1911, the Mexican government banned the killing of elephant seals and in the 1920s conducted five scientific expeditions to Isla Guadalupe (Table 10.1). Finally, in 1928 the island was decreed as a protected area.

There is no certainty about the number of elephant seals during the population bottleneck that resulted from commercial and scientific harvests. Estimates for the 1890s range from 10 to 30 (Hoelzel et al. 1993) to a few hundred individuals (Bartholomew and Hubbs 1960). The first estimate of the population size was made by Anthony (1924), who obtained an estimate of 1250 individuals using the Isla Guadalupe count of 1922 (see Table 10.1). In the following years, elephant seals were sighted at Islas San Benito, Baja California, and San Miguel Island, California. In subsequent decades (the 1940s and the 1950s), northern elephant seals expanded their distribution to other islands of Baja California, as well as to the islands of southern and central California (Bartholomew and Hubbs 1960). In 1957 the total population size was estimated at around 13,000 individuals, of which 91% were at Isla Guadalupe, 8% at Islas San Benito, and 1% at the Channel Islands, including San Miguel, Santa Barbara, and San Nicolas Islands (Bartholomew and Hubbs 1960). Stewart et al. (1994) estimated the 1991 population size at 127,000 individuals, with California colonies contributing 75% of births. The 1991 estimate calculated an overall annual rate of increase of 6.3% between 1965 and 1991; however, during that period, the colonies of California increased at an accelerated rate, while those of Baja California seemed to be stable. By 2010, the abundance of elephant seals in California was estimated at 179,000 individuals, and the population was still increasing at an average annual rate of 3.8% between 1980 and 2010 (Lowry et al. 2014), whereas in Baja California, the abundance was estimated at 22,000

Table 10.1 Northern elephant seal counts from Isla Guadalupe during the early twentieth century

Date	AM	SAM	AF	J	P	W	Total	References
1907	–	–	–	–	–	–	40	Rothschild (1910)
March 2, 1911	“Some”	“Many”	0	“Numerous”	0	6	125	Townsend (1912)
July 12, 1922	259	0	0	5	0	0	264	Anthony (1924)
July 16, 1923	361	0	0	5	0	0	366	Huey (1924)
August 30, 1924	9	109	0	6	0	0	124	Huey (1925)
June 23, 1926	363	99	0	3	0	0	465	Huey (1927)
September 28, 1929	5	0	0	464	0	0	469	Huey (1930)

AM adult males, SAM subadult males, AF adult females, J juveniles, P newborn pups, W weaned pups

individuals for 2009, but the population was decreasing at an average annual rate of 0.7% for the period 1970–2009 (García-Aguilar et al. 2018).

Currently there are ten colonies in California and five in Baja California (Lowry et al. 2014; García-Aguilar et al. 2018) (Fig. 10.4). The main breeding sites in California are located at San Miguel Island, San Nicolas Island, Santa Rosa Island, Piedras Blancas, and Año Nuevo, followed by Point Reyes, Farallon Islands, Cape San Martin/Gorda, Santa Barbara Island, and San Clemente Island (Lowry et al. 2014). In Baja California, breeding sites are located at Isla Guadalupe, Islas San Benito, Isla Cedros, Islas Coronados, and Islas Todos Santos (Arias-del-Razo et al. 2017). A few pups are occasionally born in other localities of California, such as Point Conception (Lowry et al. 2014), and Baja California, such as Natividad, San Martín, and San Jerónimo islands (Le Boeuf and Mate 1978; Franco-Ortíz 2012), as well as in Oregon, Washington, and British Columbia (Hückstädt 2015).

Breeding Season

The reproduction of the northern elephant seal is restricted in space and time. The breeding season occurs in the northern winter, and during this season, the species is highly gregarious, congregating on breeding beaches by the hundreds or thousands (Le Boeuf 1978). The mating system is extreme polygyny with establishment of harems, whose size can vary between 2 and 100 females, depending on breeding site density, characteristics of the reproductive beaches, and males' dominance (Le Boeuf 1972).

The breeding season begins with the arrival of adult males to the reproductive areas in late November or early December, depending on location, followed a few days later by the first adult females (Le Boeuf 1978). Males remain on land, fasting throughout the breeding season (mean 91 days; Deutsch et al. 1994). In contrast, females are asynchronous and are present on land for 32–34 days (Fig. 10.5) (Reiter et al. 1981; García-Aguilar 2004). Therefore, at no time of the season are all the females present on land. Females give birth to only one pup, 5–6 days after arrival (Le Boeuf 1972). Estrus occurs an average 24 days after birth and lasts around 3 days (Le Boeuf et al. 1972; García-Aguilar 2004). The mating period begins in the

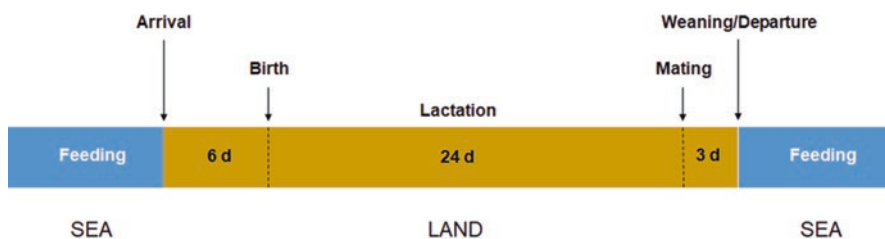


Fig. 10.5 Timeline of reproductive events during the stay on land of adult females

first week of January and ends in the first week of March, with a maximum occurring in mid-February. After mating, females leave the reproductive areas (Le Boeuf et al. 1972).

There are latitudinal differences in the occurrence of several reproductive parameters. At the Islas San Benito colony (~28°N), the first females' arrival occurs at the end of November, the first births happen in early December, and the peak of the season is in mid-January (García-Aguilar 2004). Further north, at the Año Nuevo colony (~37°N), the arrival of the first females occurs in mid-December, the first births happen around December 20, and the peak of the breeding season is at the end of January (Le Boeuf et al. 1972; Reiter et al. 1981). Despite these differences, births in both locations end at the beginning of February, and the breeding season culminates in early March. Other differences are related to natality rate, which seems to be lower at San Benito than at Año Nuevo, 74% and 84% in average, respectively (Robinson et al. 2012; Elorriaga-Verplancken and García-Aguilar 2018), and also to pre-weaning mortality rate, which was estimated at 8% in San Benito (García-Aguilar 2004) and 24% at Año Nuevo (Le Boeuf et al. 1994). Nevertheless, since these rates vary over time depending on various environmental and demographic factors, they should not be taken as fixed characteristics of the colonies.

Maternal Investment

In elephant seals, males do not provide postnatal care; thus the females' reproductive success is conditioned by their ability to obtain vital resources for themselves and their offspring. Since birth and rearing are on land, space availability is the main resource that determines the distribution of females during the breeding season (Fig. 10.6). Females prefer areas that offer protection to their pups from predators and storms and that contain resources for thermoregulation (i.e., access to water and



Fig. 10.6 Northern elephant seal female and pup. (Photo: M.C. García-Aguilar)

sandy beaches) (Le Boeuf 1991). Females form dense aggregations to prevent harassment by peripheral males, which can cause the separation of mothers from their pups, as well as serious injuries to females, and even their death (Cassini 1999).

Northern elephant seal females show embryonic diapause, or delayed implantation, which consists in keeping the embryonic development in a dormant state to delay the timing of implantation, and thus ensure that pups are born at the most favorable time for their survival (Riedman 1990). The gestation length is estimated at approximately 8 months (Le Boeuf et al. 1972; Deutsch et al. 1994). The northern elephant seal's maternal strategy is the "fasting strategy" where females arrive to reproductive areas with a large energy store in the form of blubber and fast throughout lactation (Boness and Bowen 1996). Lactation is short, averaging 27 days (Le Boeuf 1972), but the maternal investment is intense, and hence the growth rate of the pups is high. The body mass of the pups increases from 40 kg at birth to 130–140 kg at weaning, gaining on average 3.8 kg/day (Rea and Costa 1992; Crocker et al. 2001). Weaning is abrupt, and after that pups remain on land, fasting for up to 2.5 months, until they develop diving and swimming skills (Reiter et al. 1981; Le Boeuf et al. 1989). To cope with this long fasting period, the body mass of weaned pups is 42% fat and 11% protein (Crocker et al. 2001).

Elephant seal females produce nutrient-rich, energy-dense milk with fat contributing most of energy content. Since females fast throughout lactation, they use their stores for milk lipid synthesis, but they must also use the fatty acids for their own maintenance (Riedman 1979). Recent findings suggest that females preferentially use medium-chain monounsaturated fatty acids and saturated fatty acids to meet their energy requirements and long-chain monounsaturated fatty acids for milk production (Fowler et al. 2014). Milk composition changes throughout lactation as a result of both the physiological stress of the mother and the requirements of the pup: water declines from 75% after birth to 35% 2 weeks later, while fat content increases from 12% to 50% in the same period (Riedman 1979).

Adult females lose 36–37% of their body mass between their arrival and departure from the breeding areas, which represents an average of 180 kg or 7.2 kg/day (Deutsch et al. 1994; Crocker et al. 2001). Moreover, during the breeding fast, there may be an increase in oxidative damage to proteins (Sharick et al. 2015). Given the high energy cost of reproduction, it is expected that not all females will survive or breed successfully. In fact, both the probability of survival and the reproductive success of primiparous females seem to be lower than those of experienced females (Lee 2011).

Male Reproductive Effort

In all polygynous species, the variability in reproductive success is greater in males than in females (Clutton-Brock 1985), and the northern elephant seal is no exception. Male mating success is correlated with dominance rank, which in turn depends

largely on the body size and condition (Haley et al. 1991). Overall, a male of high rank is able to monopolize a large number of females (up to more than 100) in a single breeding season, while males of lower rank may mate with a minimal fraction of females (Le Boeuf 1974).

Males arrive at the reproductive areas before females and remain on land without foraging for more than 90 days, and during that period, they compete to control access to females. Initially, the social status is determined by physical confrontations, which have an extremely high energetic costs (Norris et al. 2010) and risk of lethal injuries (Fig. 10.7). Once dominance ranks have been established, they are maintained mainly by ritualized displays, which include vocalizations and body posturing (Le Boeuf 1974; Sandegren 1976; Cox 1981). These signals are usually sufficient to control the movement of subordinate males, so the frequency of physical confrontations usually decreases during the course of the breeding season.

Despite the effort that lactation represents for adult females, the energy cost for reproduction in adult males seems to be higher. Although male fasting duration over the reproductive season is three times longer than that of females, the average mass loss is similar (~36%) (Deutsch et al. 1994), but total expended energy could be three times the standard metabolic rate (Crocker et al. 2012). Moreover, the prolonged fasting of males causes oxidative damage to lipids and DNA (Sharick et al. 2015).

Unlike females, males' reproductive cost is related to both age class and social status. Average rate of mass loss is greater in adult males than in subadult males, 7.1 and 4.6 kg per day, respectively, and the percentage of body mass loss is greater in high-ranking males than in subordinates males, 41% and 34%, respectively (Deutsch et al. 1990). Also, the occurrence of external injuries, which can seriously compromise survival, is up to 20 times greater in males than in females (Deutsch et al. 1994).



Fig. 10.7 Confrontation between adult males. (Photo: M.C. García-Aguilar)

At-Sea Behavior

Northern elephant seals are deep-diving mammals that spend more than 90% of their time at sea submerged (Le Boeuf et al. 1988). Based on time-depth profiles, their dives are classified into five categories (Le Boeuf et al. 1988; Crocker et al. 1997; Kuhn et al. 2009): type A dives represent transit dives, type C food processing or rest dives, type D pelagic foraging dives, type E benthic dives used for both traveling along the continental shelf and benthic foraging, and type I short and shallow dives (<100 m).

After the post-weaning fast, weaned pups perform their first foraging migration at sea, and although the routes are not well known, some observations suggest that they move northward (Condit and Le Boeuf 1984). The mean dive depths achieved at this early stage of life is 200 m and the maximum >500 m (Le Boeuf et al. 1996). As juveniles (up to 4 years of age), elephant seals perform two migrations: one in summer, after the molt, and the second one during winter, after their resting period on land. Both female and male juveniles start their migration moving north toward the coastal waters of Washington, and then their migratory paths diverge. Females migrate toward open oceanic waters, while males remain near the continental shelf. The average dive depth is ~400 m in both sexes, with maximum dives of >600 m (Le Boeuf et al. 1996). In general, females make more transit and pelagic foraging dives than males, while males perform more benthic dives (Le Boeuf et al. 1996).

As adults, northern elephant seals alternate their stays on land to breed and molt with two migrations per year (Le Boeuf 1994). The adult females' post-breeding migration lasts 2–2.5 months (short migration), and the post-molting migration lasts 7–8 months (long migration); for adult males, both migrations last around 4 months (Le Boeuf 1994). Although both sexes migrate toward the northeast Pacific, male and female routes and destinations differ. While females exhibit similar latitudinal movements during both migrations, with a strong preference between 40° and 45°N (Robinson et al. 2012), their longitudinal movements vary seasonally. During the short migration, females travel over 5000 km and remain east of 160°W, while in the long migration, they can travel near 180°E, covering a distance of ~10,000 km (Fig. 10.8) (Robinson et al. 2012). Despite this difference in the routes between migrations, their transit speed is similar, ranging from 40 to 65 km/day (Le Boeuf et al. 2000). All these findings come from satellite tracking studies conducted on animals from California, but isotopic data from adult females at the San Benito colony indicates they forage ~8° south of those from California (Aurioles et al. 2006). Males travel about 10,000 km during each migration, moving further north than females and foraging in the Gulf of Alaska and near the Aleutian Islands, between 42 and 58°N (Fig. 10.9) (Stewart and DeLong 1995; Le Boeuf et al. 2000). Their average transit speed is around 85 km/d (Le Boeuf et al. 2000).

Adult female mean dive depth is approximately 500 m, with maximum dives greater than 1500 m (Robinson et al. 2012; Hückstädt et al. 2018). Overall, females spend more time at sea on transit and foraging dives (types A and D), while benthic dives and shallow dives (types E and I) are usually uncommon (Le Boeuf et al.

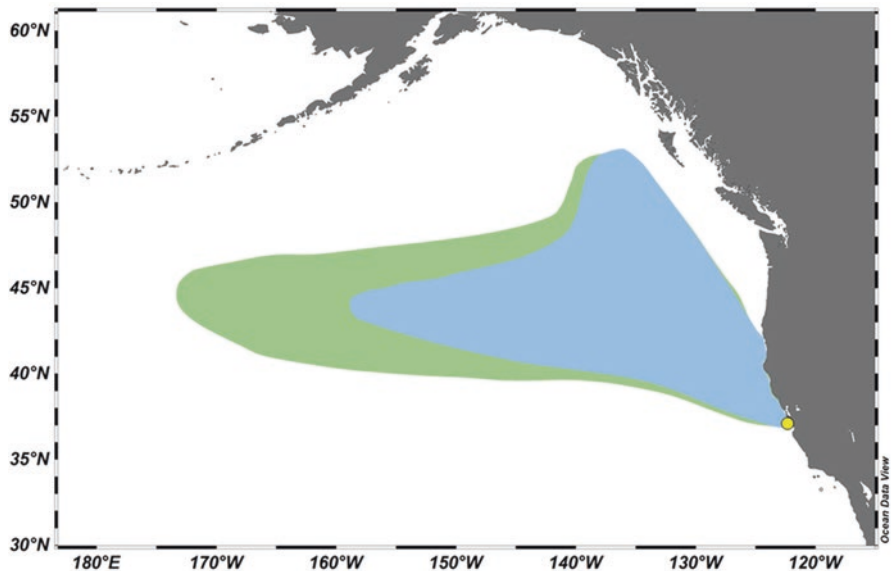


Fig. 10.8 Post-breeding (blue) and post-molting (green) migratory paths of northern elephant seal females from Año Nuevo, California (yellow dot). Based on Robinson et al. (2012)

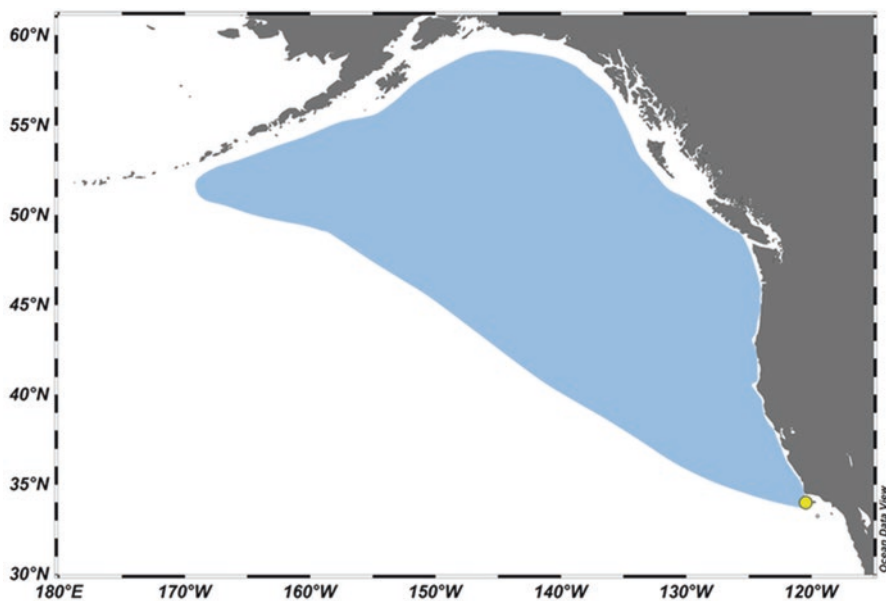


Fig. 10.9 Migratory paths of northern elephant seal males from San Miguel Island, California (yellow dot). Based on Stewart and DeLong (1994)

2000; Kuhn et al. 2009; Robinson et al. 2012). The dives of adult males are longer than those of adult females (~20%) but with a lower mean dive depth, which ranges from 350 to 450 m (DeLong and Stewart 1991). Moreover, type D dives are less frequent than in females, and type E dives are more frequent (Le Boeuf 1994).

Diet

Elephant seals do not chew food but instead swallow prey (Antonelis et al. 1987; Abbott and Verstraete 2005); therefore, it is likely that they use suction to feed on small prey of <15 cm length and/or < 70 g weight (Naito et al. 2013; Adachi et al. 2019). The diet of the northern elephant seal is not well understood, but diving patterns and isotopic data suggest that there are sexual differences both in feeding strategies and in the type of prey. That is, females seem to consume mainly epi- and mesopelagic prey of wide distribution, while males appear to preferably consume benthic prey in localized areas of the continental shelf (Le Boeuf et al. 2000; Riofrío-Lazo et al. 2012).

Elephant seals have traditionally been assumed to feed primarily on squid. Antonelis et al. (1994) identified more than 28 species of squid as part of the diet, being the most important prey *Octopoteuthis deletron*, *Histioteuthis heteropsis*, *Stigmatheuthis dofleini*, and *Gonatopsis borealis*, although the Pacific hake, *Merluccius productus*, and the tuna crab, *Pleuroncodes planipes*, also contributed notably. However, a recent study indicates that the diet consists mainly of mesopelagic fishes, particularly myctophids such as *Tarletonbeania taylori* and *Electrona risso*; non-migratory species of squid are also an important component of the diet, especially *Chiroteuthis* c.f. *calyx* and *S. dofleini* (Goetsch 2018). The discrepancies between these studies could be due to the sampling and analyses. Antonelis et al. (1994) collected stomach contents from adult and subadult males and from adult females for the identification of remains (otoliths and squid beaks), while Goetsch (2018) collected biopsies only from adult females for the analysis of fatty acid signatures. On the other hand, stomach contents were collected around two decades earlier than biopsies; therefore, the difference in diet could be due also to temporal variation in prey availability.

Conservation Status and Threats

The northern elephant seal was almost driven to extinction by overhunting for its oil in the nineteenth century, leaving a few individuals who took refuge at Isla Guadalupe. After being protected by Mexican law in the early twentieth century, the species began to recover during the first half of the century and is currently located in all areas of its known historical distribution. At the beginning of the twenty-first century, the northern elephant seal population was estimated at approximately

201,000 individuals, of which 90% are in California, USA, and 10% in Baja California, Mexico. However, the numbers in California are increasing, while those in Baja California are decreasing (Lowry et al. 2014; García-Aguilar et al. 2018).

The northern elephant seal is currently listed as a species of *Least Concern* in the Red List of Threatened Species of the International Union for Conservation of Nature (IUCN) (Hückstädt 2015). In 1992 the species was removed from Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). In the United States, it is protected by the Marine Mammal Protection Act, but is not considered a strategic stock, and is not listed as *Endangered* or *Threatened* by the Endangered Species Act. In Mexico, elephant seals are protected under the Norma Oficial Mexicana NOM-059-ECOL-2010, and all their breeding and haul-out sites in Baja California are in protected areas decreed by the Mexican government. Although there are movements of individuals between the colonies of Baja California and California, there are no international agreements for the management of the species between the governments of Mexico and the United States.

Unlike many other pinniped species, incidental fishery mortality is very low, approaching a zero rate in US fisheries (Carretta et al. 2017), but incidental fishery mortality rate is not known in Mexico. In recent times, there has been an increase in the number of entangled animals (which can potentially die), presumably related to the “Great Pacific Garbage Patch” (Hückstädt 2015), located in waters between California and Hawaii (Lebreton et al. 2018).

Oceanographic anomalies, such as El Niño Southern Oscillation and recently the 2013–2016 warm water anomaly (“The Blob”; Kintisch 2015), impact pinniped populations. For the northern elephant seal, the most notable effects are increased pup mortality, reduced juvenile survival, low reproductive success of females, and increased foraging effort by adult females (Le Boeuf and Reiter 1991; Crocker et al. 2006). However, perhaps the greatest threat to the northern elephant seal is its low genetic diversity, a consequence of the population bottleneck they went through (Hoelzel et al. 2002; Abadía-Cardoso et al. 2017). The lack of genetic diversity makes the northern elephant seal population highly vulnerable to infectious diseases and environmental changes (Hückstädt 2015).

Although no disease outbreaks have been reported so far, several pathogens have been detected in both captive and free-ranging northern elephant seals. Bacteria such as *Leptospira* sp. (Colegrove et al. 2005; Serrano-de-la-Vega 2012), *Escherichia coli*, *Streptococcus* sp., and *Enterococcus* sp. (Spraker et al. 2014) have been isolated, as well as various viruses such as caliciviruses (Kennedy-Stoskopf 2001), gammaherpesvirus (Goldstein et al. 2006), and H1N1 influenza virus (Goldstein et al. 2013). Infections by the *Otostrongylus circumlitus* nematode have also been reported (Elson-Riggins et al. 2001).

Climate change appears as another major concern, because of the increased sea surface temperature (SST) resulting in nutritional stress (Le Boeuf and Crocker 2005) and disrupting the northern elephant seal’s ability to thermoregulate while on land (Noren 2002). Climate projections predict that both the SST and air temperatures will increase above current and historical levels (IPCC 2014). Under those

conditions, heat becomes an environmental threat, especially for northern elephant seal pups because of their diminished heat tolerance that makes them highly susceptible to hyperthermia (or heat stroke), potentially leading to death (Salogni et al. 2015).

References

- Abadía-Cardoso A, Freimer NB, Deiner K et al (2017) Molecular population genetics of the northern elephant seal *Mirounga angustirostris*. *J Hered* 108(6):618–627
- Abbott C, Verstraete RJM (2005) The dental pathology of northern elephant seals (*Mirounga angustirostris*). *J Comp Pathol* 132(2–3):169–178
- Adachi T, Hückstädt LA, Tift MS et al (2019) Inferring prey size variation from mandible acceleration in northern elephant seals. *Mar Mamm Sci* 35(3):893–908
- Anthony AW (1924) Notes on the present status of the northern elephant seal, *Mirounga angustirostris*. *J Mammal* 5(3):145–152
- Antonelis GA, Lowry MS, Fiscus CH (1987) Assessing northern elephant seal feeding habits by stomach lavage. *Mar Mamm Sci* 3(4):308–322
- Antonelis GA, Lowry MS, Fiscus CH et al (1994) Diet of the northern elephant seal. In: Le Boeuf BJ, Laws RM (eds) *Elephant seals: population ecology, behavior and physiology*. University of California Press, Berkeley/Los Angeles/Oxford, pp 211–223
- Arias-Del-Razo A, Schramm Y, Heckel G et al (2017) Distribution of four pinnipeds (*Zalophus californianus*, *Arctocephalus philippii townsendi*, *Phoca vitulina richardii*, and *Mirounga angustirostris*) on islands off the west coast of the Baja California Peninsula, Mexico. *Aquat Mamm* 43(1):40–51
- Aurioles D, Koch PL, Le Boeuf BJ (2006) Differences in foraging location of Mexican and California elephant seals: evidence from stable isotopes in pups. *Mar Mamm Sci* 22(2):326–338
- Bartholomew GA, Hubbs CL (1960) Population growth and seasonal movements of the northern elephant seal, *Mirounga angustirostris*. *Mammalia* 24(3):313–324
- Boness DJ, Bowen WD (1996) The evolution of maternal care in pinnipeds. *Bioscience* 46(9):645–654
- Carretta, JV, Forney KA, Oleson E et al (2017) U.S. Pacific marine mammal stock assessments, 2016. NOAA Technical memorandum 577
- Cassini MH (1999) The evolution of reproductive systems in pinnipeds. *Behav Ecol* 10(5):612–616
- Clinton WL, Le Boeuf BJ (1993) Sexual selection's effects on male life history and the pattern of male mortality. *Ecology* 74(6):1884–1892
- Clutton-Brock TH (1985) Selection in relation to sex. In: Bendall S (ed) *Evolution from molecules to men*. Cambridge University Press, Cambridge, pp 457–481
- Codde SA, Allen SG, Houser DS, Crocker DE (2016) Effects of environmental variables on surface temperature of breeding female northern elephant seals, *Mirounga angustirostris*, and pups. *J Therm Biol* 61:98–105
- Colegrove KM, Lowenstine LJ, Gulland FMD (2005) Leptospirosis in northern elephant seals (*Mirounga angustirostris*) stranded along the California coast. *J Wildlife Dis* 41(2):426–430
- Condit R, Le Boeuf BJ (1984) Feeding habits and feeding grounds of the northern elephant seal. *J Mammal* 65(2):281–290
- Condit R, Reiter J, Morris PA et al (2013) Lifetime survival rates and senescence in northern elephant seals. *Mar Mamm Sci* 30(1):122–138
- Cox CR (1981) Agonistic encounters among male elephant seals: frequency, context, and the role of female preference. *Am Zool* 21:197–209
- Crocker DE, Le Boeuf BJ, Costa DP (1997) Drift diving in female northern elephant seals: implications for food processing. *Can J Zool* 75:27–39

- Crocker DE, Williams JD, Costa DP et al (2001) Maternal traits and reproductive effort in northern elephant seals. *Ecology* 82(12):3451–3555
- Crocker DE, Costa DP, Le Boeuf BJ et al (2006) Impact of El Niño on the foraging behavior of female northern elephant seals. *Mar Ecol Prog Ser* 309:1–10
- Crocker DE, Houser DS, Webb PM (2012) Impact of body reserves on energy expenditure, water flux, and mating success in breeding male northern elephant seals. *Physiol Biochem Zool* 85(1):11–20
- De Muizon C (1982) Phocid phylogeny and dispersal. *Ann S Afr Mus* 89(2):175–213
- DeLong RL, Stewart BS (1991) Diving patterns of northern elephant seal bulls. *Mar Mamm Sci* 7(4):369–384
- Deméré TA, Berta A, Adam PJ (2003) Pinnipedimorph evolutionary biogeography. *B Am Mus Nat Hist* 279:32–76
- Deutsch CJ, Haley MP, Le Boeuf BJ (1990) Reproductive effort of male northern elephant seals: estimates from mass loss. *Can J Zool* 68:2580–2593
- Deutsch CJ, Crocker DE, Costa DP et al (1994) Sex- and age-related variation in reproductive effort of northern elephant seals. In: Le Boeuf BJ, Laws RM (eds) *Elephant seals: population ecology, behavior, and physiology*. University of California Press, Berkeley/Los Angeles/Oxford, pp 169–210
- Elorriaga-Verplancken F, García-Aguilar MC (2018) Inter-annual (2002–2016) variation on the natality rate of the northern elephant seal (*Mirounga angustirostris*) at the San Benito colony, Baja California, Mexico. *Mar Mamm Sci* 34(3):823–828
- Elson-Riggins JC, Al-Banna L, Platzer EG et al (2001) Characterization of *Otostrongylus circumlitus* from Pacific harbor and northern elephant seals. *J Parasitol* 87(1):73–78
- Fowler MA, Debier C, Mignolet E et al (2014) Fatty acid mobilization and comparison to milk fatty acid content in northern elephant seals. *J Comp Physiol B* 184:284–294
- Franco-Ortiz M (2012) Distribución y abundancia del elefante marino del norte, *Mirounga angustirostris*, en México. Dissertation, Universidad Autónoma de Baja California
- Fyler CA, Reeder TW, Berta A et al (2005) Historical biogeography and phylogeny of monachine seals (Pinnipedia: Phocidae) based on mitochondrial and nuclear DNA data. *J Biogeogr* 32:1267–1279
- García-Aguilar MC (2004) Breeding biology of the northern elephant seal (*Mirounga angustirostris*) at the Isla San Benito del Oeste, Eastern Pacific, Mexico. *Aquat Mamm* 30(2):289–295
- García-Aguilar MC, Turrent C, Elorriaga-Verplancken F et al (2018) Climate change and the northern elephant seal (*Mirounga angustirostris*) population in Baja California, Mexico. *PLoS One* 13(2):e0193211
- Gill T (1866) Prodrôme of a monograph of the pinnipeds. *Proc Essex Inst* 5:3–13
- Goetsch C (2018) Illuminating the twilight zone: diet and foraging strategies of a deep-sea predator, the northern elephant seal. Ph.D. Dissertation, University of California Santa Cruz
- Goldstein T, Lowenstine LJ, Lipscomb TP et al (2006) Infection with a novel gammaherpesvirus in northern elephant seals (*Mirounga angustirostris*). *J Wildlife Dis* 42(4):830–835
- Goldstein T, Mena I, Anthony SJ et al (2013) Pandemic H1N1 influenza isolated from free-ranging northern elephant seals in 2010 off the Central California coast. *PLoS One* 8(5):e62259
- Haley MP, Deutsch CJ, Le Boeuf BJ (1991) A method for estimating mass of large pinnipeds. *Mar Mamm Sci* 7(2):157–164
- Hindell MA, Perrin W (2008) Elephant seals, *Mirounga angustirostris* and *M. leonine*. In: Würsig B, Perrin W, Thewissen JGM (eds) *Encyclopedia of marine mammals*, 2nd edn. Academic Press, Burlington/San Diego/New York/London, pp 364–368
- Hoelzel AR, Halley J, Campagna C et al (1993) Elephant seal genetic variation and the use of simulation models to investigate historical population bottlenecks. *J Hered* 84(6):443–449
- Hoelzel AR, Fleischer RC, Campagna C et al (2002) Impact of a population bottleneck on symmetry and genetic diversity in the northern elephant seal. *J Evol Biol* 15(4):567–575
- Hückstädt L (2015) *Mirounga angustirostris*. In: The IUCN red list of threatened species. <https://doi.org/10.2305/IUCN.UK.2015-2.RLTS.T13581A45227116.en>. Accessed 19 Nov 2019

- Hückstädt LA, Holser RR, Tift MS et al (2018) The extra burden of motherhood: reduced dive duration associated with pregnancy status in a deep-diving mammal, the northern elephant seal. *Biol Lett* 14:20170722
- Huey LM (1924) Recent observations on the northern elephant seal. *J Mammal* 5(4):237–242
- Huey LM (1925) Late information on the Guadalupe Island elephant seal herd. *J Mammal* 6(2):126–127
- Huey LM (1927) The latest northern elephant seal census. *J Mammal* 8(2):160–161
- Huey LM (1930) Past and present status of the northern elephant seals with a note on the Guadalupe fur seal. *J Mammal* 11(2):188–194
- Intergovernmental Panel on Climate Change (IPCC) (2014) *Climate change 2014: synthesis report*. Geneva
- Kennedy-Stoskopf S (2001) Viral diseases. In: Dierauf LA, Gulland FMD (eds) *CRC handbook of marine mammal medicine*, 2nd edn. Taylor & Francis Group, Boca Raton, pp 285–308
- Khamas WA, Smoldlaka H, Leach-Robinson J et al (2012) Skin histology and its role in heat dissipation in three pinniped species. *Acta Vet Scand* 54(1):46
- Kintisch E (2015) ‘The blob’ invades Pacific, flummoxing climate experts. *Science* 348:17–18
- Kuhn CE, Crocker DE, Tremblay Y et al (2009) Time to eat: measurements of feeding behaviour in a large marine predator, the northern elephant seal *Mirounga angustirostris*. *J Anim Ecol* 78:515–523
- Le Boeuf BJ (1972) Sexual behaviour in the northern elephant seal, *Mirounga angustirostris*. *Behaviour* 41(1):1–1)26
- Le Boeuf BJ (1974) Male-male competition and reproductive success in elephant seals. *Am Zool* 14:163–176
- Le Boeuf BJ (1978) Social behavior in some marine and terrestrial carnivores. In: Reese ES, Lighter FJ (eds) *Contrast in behaviour*. Wiley, Hoboken, pp 251–279
- Le Boeuf BJ (1991) Pinniped mating systems on land, ice and the water: emphasis on the Phocidae. In: Renouf D (ed) *Behavior of pinnipeds*. Chapman and Hall, London, pp 45–65
- Le Boeuf BJ (1994) Variation in the diving pattern of northern elephant seals with age, mass, sex, and reproductive condition. In: Le Boeuf BJ, Laws RM (eds) *Elephant seals: population ecology, behavior and physiology*. University of California Press, Berkeley/Los Angeles/Oxford, pp 237–252
- Le Boeuf BJ, Crocker DE (2005) Ocean climate and seal condition. *BMC Biol* 3:9
- Le Boeuf BJ, Laws RM (1994) Elephant seals: an introduction to the genus. In: Le Boeuf BJ, Laws RM (eds) *Elephant seals: population ecology, behavior, and physiology*. University of California Press, Berkeley/Los Angeles/Oxford, pp 1–26
- Le Boeuf BJ, Mate BR (1978) Elephant seal colonize additional Mexican and California islands. *J Mammal* 59(3):621–622
- Le Boeuf BJ, Reiter J (1991) Biological effects associated with El Niño southern oscillation, 1982–83, on northern elephant seals breeding at Año Nuevo, California. In: Trillmich F, Ono KA (eds) *Pinnipeds and El Niño, ecological studies*, vol 88. Springer, Berlin/Heidelberg, pp 206–218
- Le Boeuf BJ, Whiting RJ, Gantt RF (1972) Perinatal behavior of northern elephant seal females and their young. *Behaviour* 43(1):121–156
- Le Boeuf BJ, Costa DP, Huntley AC et al (1988) Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Can J Zool* 66:446–458
- Le Boeuf BJ, Condit R, Reiter J (1989) Parental investment and the secondary sex ratio in northern elephant seals. *Behav Ecol Sociobiol* 25(2):109–117
- Le Boeuf BJ, Morris P, Reiter J (1994) Juvenile survivorship of northern elephant seals. In: Le Boeuf BJ, Laws RM (eds) *Elephant seals: population ecology, behavior and physiology*. University of California Press, Berkeley/Los Angeles/Oxford, pp 121–136
- Le Boeuf BJ, Morris PA, Blackwell SB et al (1996) Diving behavior of juvenile northern elephant seals. *Can J Zool* 74:1632–1644

- Le Boeuf BJ, Crocker DE, Costa DP et al (2000) Foraging ecology of northern elephant seals. *Ecol Monogr* 70(3):353–382
- Lebreton L, Slat B, Ferrari F et al (2018) Evidence that the great Pacific garbage patch is rapidly accumulating plastic. *Sci Rep UK* 8:4666
- Lee DE (2011) Effects of environmental variability and breeding experience on northern elephant seal demography. *J Mammal* 92(3):517–526
- Lowry MS, Condit R, Hatfield B et al (2014) Abundance, distribution, and population growth of the northern elephant seal (*Mirounga angustirostris*) in the United States from 1991 to 2010. *Aquat Mamm* 40(1):20–31
- Mauck B, Bilgmann K, Jones DD et al (2003) Thermal windows on the trunk of hauled seals: hot spots for thermoregulatory evaporation? *J Exp Biol* 202:1727–1738
- Naito Y, Costa DP, Adachi T et al (2013) Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. *Funct Ecol* 27:710–717
- Noren DP (2002) Thermoregulation of weaned northern elephant seal (*Mirounga angustirostris*) pups in air and water. *Physiol Biochem Zool* 75(5):513–523
- Norris AL, Houser DS, Crocker DE (2010) Environment and activity affect skin temperature in breeding adult male elephant seals (*Mirounga angustirostris*). *J Exp Biol* 213:4205–4212
- Ray CE (1976) Geography of phocid evolution. *Syst Zool* 25:391–406
- Rea LD, Costa DP (1992) Changes in standard metabolism during long-term fasting in northern elephant seal pups (*Mirounga angustirostris*). *Physiol Zool* 65:97–111
- Reiter J, Panken KJ, Le Boeuf BJ (1981) Female competition and reproductive success in northern elephant seals. *Anim Behav* 29:670–687
- Riedman M (1979) Changes in milk composition during lactation in the northern elephant seal. *Physiol Zool* 52(2):240–249
- Riedman M (1990) The pinnipeds: seals, sea lions, and walruses. University of California Press, Berkeley/Los Angeles/Oxford
- Riofrío-Lazo M, Aurióles-Gamboa D, Le Boeuf BJ (2012) Ontogenetic changes in feeding habits of northern elephant seals revealed by $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ analysis of growth layers in teeth. *Mar Ecol Progr Ser* 450:229–224
- Robinson PW, Costa DP, Crocker DE et al (2012) Foraging behavior and success of a mesopelagic predator in the Northeast Pacific Ocean: insights from a data-rich species, the northern elephant seal. *PLoS One* 7(5):e36728
- Rothschild W (1910) Notes on sea elephants (*Mirounga*). *Novitates Zoologicae* 17(3):445–446
- Salogni E, Sanvito S, Galimberti F (2015) Postmortem examination and causes of death of northern elephant seal (*Mirounga angustirostris*) pups at the San Benito Islands, Baja California, Mexico. *Mar Mamm Sci* 32(2):743–752
- Salogni E, Galimberti F, Sanvito S et al (2018) Male and female pups of the highly sexually dimorphic northern elephant seal (*Mirounga angustirostris*) differ slightly in body size. *Can J Zool* 97:241–250
- Sandegren FE (1976) Agonistic behavior in the male northern elephant seal. *Behavior* 57(1–2):136–158
- Scammon CM (1870) Sea-elephant hunting. *Overland Mon* 4(2):112–117
- Serrano-de-la-Vega MI (2012) Exposición a *Leptospira* sp. patógena del elefante marino, *Mirounga angustirostris*. Dissertation, Universidad Autónoma de Baja California
- Sharick JT, Vasquez-Medina JP, Ortiz RM et al (2015) Oxidative stress is a potential cost of breeding in male and female northern elephant seals. *Funct Ecol* 29(3):367–376
- Spraker TR, Lyons ET, Kuzmina TA et al (2014) Causes of death in preweaned northern elephant seal pups (*Mirounga angustirostris*, Gill, 1866), Año Nuevo State Reserve, California, 2012. *J Vet Diagn Invest* 26(2):320–326
- Stewart BS, DeLong RL (1994) Postbreeding foraging migration of northern elephant seals. In: Le Boeuf BJ, Laws RM (eds) *Elephant seals: population ecology, behavior and physiology*. University of California Press, Berkeley/Los Angeles/Oxford, pp 291–309

- Stewart BS, DeLong RL (1995) Double migrations of the northern elephant seal, *Mirounga angustirostris*. *J Mammal* 76(1):196–205
- Stewart BS, Huber HR (1993) *Mirounga angustirostris*. *Mamm Species* 449:1–10
- Stewart BS, Yochem PK, Huber HR et al (1994) History and present status of the northern elephant seals population. In: Le Boeuf BJ, Laws RM (eds) *Elephant seals: population ecology, behavior and physiology*. University of California Press, Berkeley/Los Angeles/Oxford, pp 29–48
- Sydeman WJ, Nur N (1994) Life history strategies of female northern elephant seals. In: Le Boeuf BJ, Laws RM (eds) *Elephant seals: population ecology, behavior and physiology*. University of California Press, Berkeley/Los Angeles/Oxford, pp 137–153
- Sydeman WJ, Huber HR, Emslie SD et al (1991) Age-specific weaning success of northern elephant seals in relation to previous breeding experience. *Ecology* 72(6):2204–2217
- Tennett KA, Costa DP, Nicastro AJ et al (2018) Terrestrial locomotion of the northern elephant seal (*Mirounga angustirostris*): limitation of large aquatically adapted seals on land? *J Exp Biol* 221:jeb180117
- Townsend CH (1885) An account of recent captures of the California Sea-elephant and statistics related to the present abundance of the species. *Proc US Nat Mus* 8:90–94
- Townsend CH (1912) The northern elephant seal, *Macrorhinus angustirostris* Gill. *Zoologica* 1(8):159–173