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Mirounga angustirostris.

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Mirounga angustirostris (Gill, 1866*a*)

Northern Elephant Seal

Macrorhinus angustirostris Gill, 1866*a*:13. Type locality "California". Gill (1866*b*:33) further identified the type locality as "St. Bartholomew's Bay, Lower California" (= Bahia San Bartolome, Baja California Sur, Mexico).

Morunga angustirostris: Gray, 1871:5. Name combination.

C[*ystophora*]. *angustirostris*: Peters, 1875:394. Name combination.

[*Mirounga*] *angustirostris*: Elliot, 1904:545. First use of current name combination.

Mirounga leonina leonina: Rothschild, 1910:446 (part). Name combination; not *Mirounga leonina* (Linnaeus, 1758).

CONTEXT AND CONTENT. Order Carnivora, Suborder Pinnipedia, Family Phocidae, Subfamily Monachinae. Tribe Miroungini. The genus *Mirounga* has two species, *M. leonina* in the Southern Hemisphere and *M. angustirostris* in the Northern Hemisphere. *M. angustirostris* is monotypic.

DIAGNOSIS. *Mirounga angustirostris* is distinguished from most other phocids by its incisor formula (2/1), the simple postcanine teeth, and the long proboscis of adult males (Fig. 1)—characters that are similar to those of *Cystophora* (King, 1966; Kovacs and Lavigne, 1986). *Mirounga angustirostris* resembles *Monachus* in the simple, countershaded, unspotted pelage and in the catastrophic molt during which the hair is shed along with the cornified epidermis in large patches. The teeth are small with single root, the hind feet lack nails, the nose of the adult male is elongated into a tubular proboscis capable of dilation and extension, and the palate is short and emarginate (Elliott, 1904). Gill (1866*b*) described the general cranial features of a female northern elephant seal and compared them to similar features of a southern elephant seal (*M. leonina*) which he believed also to be female. Further, he distinguished the northern and southern species from this comparison, based on the narrower snout and different form of the palatine bones of the former. It was later determined, however, that the specimen from the southern hemisphere was in fact a young male (Flower, 1881).

GENERAL CHARACTERS. The superior outline of the skull is irregularly arched from the lambdoidal suture to the end of the nasals (Figs. 2, 3). The snout of the male is lengthened, narrowed at the end, widest behind the last molar and equal to 3.5 times the total length of the skull. The adult cranium is relatively massive with heavy, broad zygomata with a long interorbital area and a broad snout. The adult female skull is considerably smaller and more delicate than that of the male (King, 1972). The squamosal is truncate above the meatus auditorius. The palatines are short and the posterior sinus is semi-oval, the bottom of the sinus being about midway between the snout and the line of the jugular foramina. The maxillae are deeply incurved and the line of the molars is incurved. There is a group of vibrissae over each eye. The hind flippers are emarginate, hairy, and lack nails (Elliot, 1904).

Females grow to 280–300 cm (standard length) and 600–800 kg and males grow to 380–410 cm (standard length) and 2,300 kg. Adult dentition is i 2/1, c 1/1, pc 5/5, total 30, although the number of postcanines may vary from three to seven, especially in the mandibles (Allen, 1880; Briggs, 1974; Briggs and Morejohn, 1975, 1976). The postcanines are simple and peg-like and relatively nonfunctional; the canines are sexually dimorphic in size and shape (Briggs, 1974; Briggs and Morejohn, 1975).

DISTRIBUTION. Makah Indians along the Washington Coast traditionally hunted elephant seals each spring near the Strait of Juan de Fuca, British Columbia (Cowan and Carl, 1945). Aborigines hunted, and perhaps overexploited, northern elephant seals on the southern California Channel Islands and on the nearby California mainland in prehistoric times, perhaps as early as 11,000 years ago (Lyon, 1937; Stewart et al., in press *a*; Walker and Craig, 1979). The species was extirpated from the central California coast and the southern California Channel Islands and was reduced to small numbers on the islands off Baja California by sealers, whalers, and sea otter (*Enhydra lutris*) hunters in the 1800s. The species was thought extinct about 1880, but was rediscovered on Isla de Guadalupe, Baja California, in 1892 (Bartholomew and Hubbs, 1960; Townsend, 1912). The abundance of the species prior to commercial exploitation is unknown, but breeding colonies existed at San Cristobol Bay and Isla de Guadalupe, at least (Scammon, 1869, 1874; Townsend, 1912). The absolute abundance of the species when sealing activities, and then scientific collections, terminated is also unknown, but there may have been fewer than several hundred seals alive in the early 1900s (Bartholomew and Hubbs, 1960). Beginning in the early 1900s, northern elephant seals began a well-documented increase in abundance (Bartholomew and Hubbs, 1960; Cooper and Stewart, 1983; Stewart, 1989; Stewart et al., in press *a*, in press *b*). Accompanying this increasing abundance was an expansion of the non-breeding and breeding ranges northward from the surviving remnant population at Isla de Guadalupe (Fig. 4). Seals were observed during non-breeding seasons in California, Oregon, and Washington waters in the early and mid-1900s (Anonymous, 1939; Anthony, 1924; Bartholomew, 1950; Bonnot et al., 1938; Freiburg and Dumas, 1954; Mate, 1969, 1970; Rett, 1952; Rowly, 1921). In U.S.A. waters, breeding began at San Miguel, San Nicolas, and Santa Barbara islands in the early 1950s (Bartholomew and Boolootian, 1960; Odell, 1974; Stewart, 1989), at Año Nuevo Island in 1961 (Radford et al., 1965), at Southeast Farallon Island in 1972 (Le Boeuf et al., 1974), on the mainland at Año Nuevo Point in 1975 (Le Boeuf and Panken, 1977), and at Santa Rosa Island in 1985 (Stewart and Yochem, 1986). A few pups have been born, sporadically, at San Clemente Island since 1977, and in recent years a few have been born at mainland central California sites at Point Reyes, Cape San Martin/Gorda, and Point St. George (Allen et al., 1989; Stewart and Yochem, 1986; Stewart et al., in press *b*). In 1991, northern elephant seals were estimated to number around 127,000 (Stewart et al., in press *b*).

Small, but increasing, numbers of seals haul out along the coasts of northern California and Oregon from spring through autumn (King et al., 1989; Stewart, 1989; Sullivan, 1980). Several northern elephant seals were seen along the eastern Aleutian islands in 1977 and 1978, two juveniles were reported at Midway Island in the

FIG. 1. Photo of *M. angustirostris* adult male, adult female, and nursing young at San Miguel Island, California.

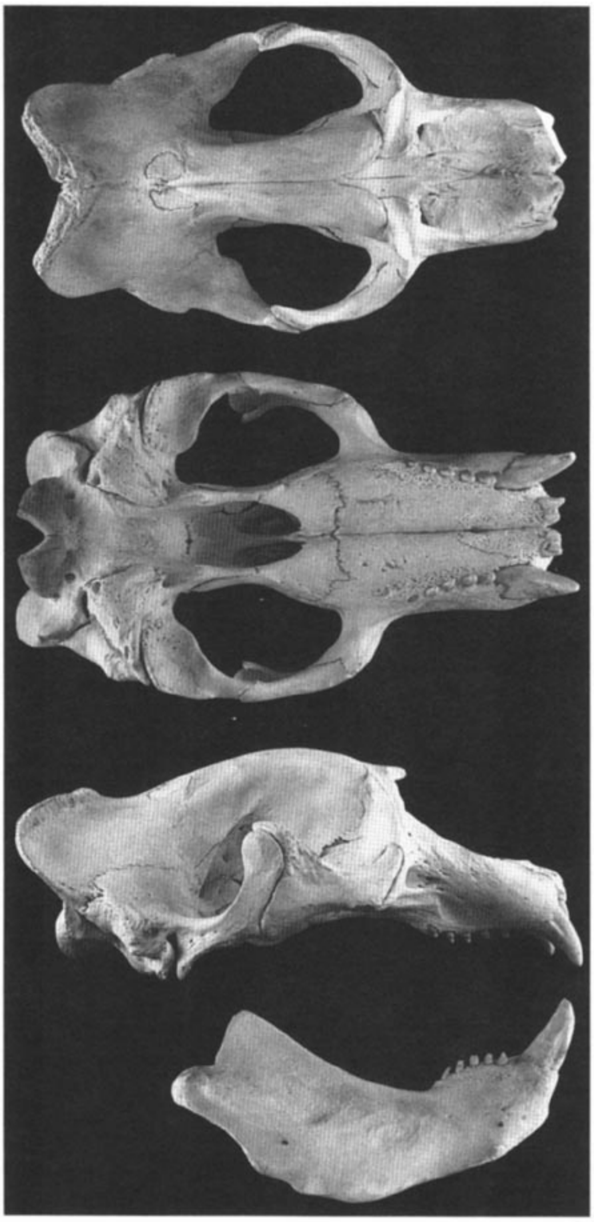

FIG. 2. Cranium of adult male *Mirounga angustirostris* in dorsal, ventral, and lateral views, and lateral view of mandible (condylobasal length is 46.4 cm). Photos by M. Muto.

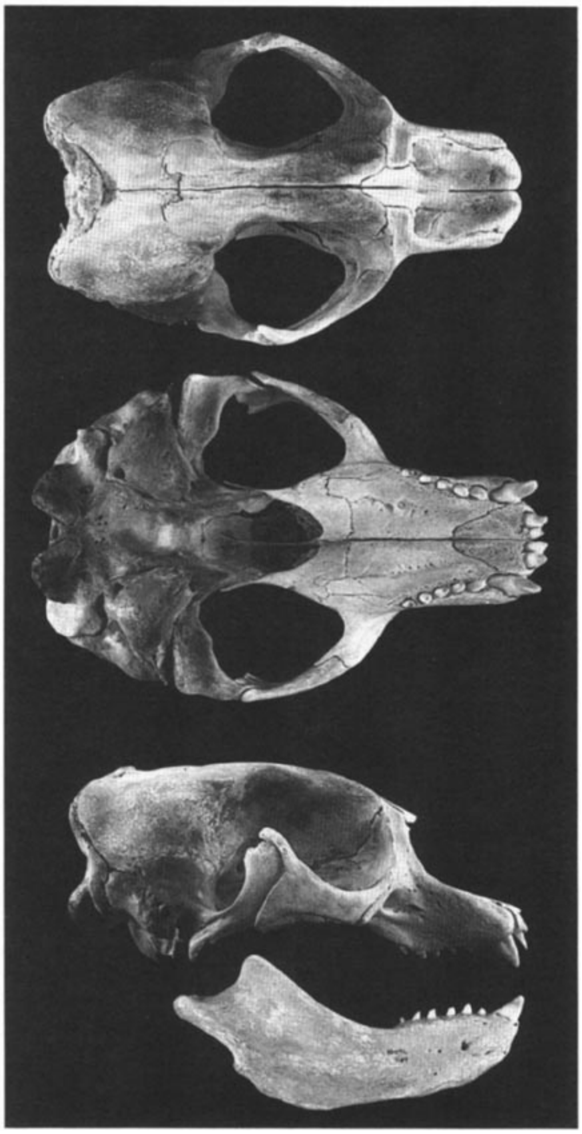

FIG. 3. Cranium of female *Mirounga angustirostris* in dorsal, ventral, and lateral views, and lateral view of mandible (condylobasal length is 34.6 cm). Photos by M. Muto.

northwestern Hawaiian Islands (Antonelis and Fiscus, 1980), and a juvenile male hauled out on Niijima Island (34°20'N, 139°15'E), near Japan, in 1989 (Kiyota et al., 1992).

Recent studies have shown that northern elephant seals range widely in the North Pacific when they are not ashore during brief periods to breed and molt. Adult males range into the Gulf of Alaska and along the Alaska peninsula and eastern Aleutian Islands whereas females remain further south between 40-45°N latitude and as far west as 173°W longitude (DeLong et al., 1992; Stewart and DeLong, in press *a*, in press *b*). Adults remain far offshore while migrating and foraging whereas juveniles and subadult males are reported often in nearshore waters of Oregon, Washington, and British Columbia during some seasons (Condit and Le Boeuf, 1984; Cowan and Carl, 1945; Freiburg and Dumas, 1954; Scheffer and Kenyon, 1963; Willett, 1943).

FOSSIL RECORD. Recent fossil evidence supports the view that the monachine *Callophoca* group, which occurred in the Carribean in the Miocene, passed through the Central American Seaway (by at least 5×10^6 years ago) prior to its closure in the early Pliocene and gave rise to the *Mirounga* lineage in the Pacific about 3-4 $\times 10^6$ years ago (Hendey, 1972; de Muizon, 1982; de Muizon and Hendey, 1980; Ray, 1976; Repenning et al., 1979). Presumably, with the subsequent cooling of the Central American Pacific during the Pleistocene, representatives of this lineage crossed the equator and dispersed southward along the west coast of South America; disruption of genetic exchange, perhaps by warming of the equatorial Pacific, may have isolated Northern and Southern Hemisphere populations with later divergence giving rise to *M. angustirostris* in the Northern Hemisphere along the Pacific coast of North America and *M. leonina* in the Southern Hemisphere along the western coast of South America and on the subantarctic islands. The earliest confirmed records of *Mirounga* in the North Pacific are from late Pleistocene rocks of southern California (Barnes and Mitchell, 1975; Ray, 1976) and no records are known for the Southern Hemisphere. Hendey (1972) thought that the genus probably arose during the Pliocene and that the present distribution developed during the Pleistocene.

FORM AND FUNCTION. There are 39-40 vertebrae; 7 C, 15 T, 5 L, 3 S, and 9 or 10 Ca (Davidson, 1929). The hypapophysial tubercle of the atlas is well developed, and the lateral laminae are depressed apically causing the outline of the lower margin to be sinuous. The anterior articular surfaces of the axis are narrow. A ventral keel is present only on the anterior and posterior vertebrae. The lumbar vertebrae are slightly flattened, or, in some cases have

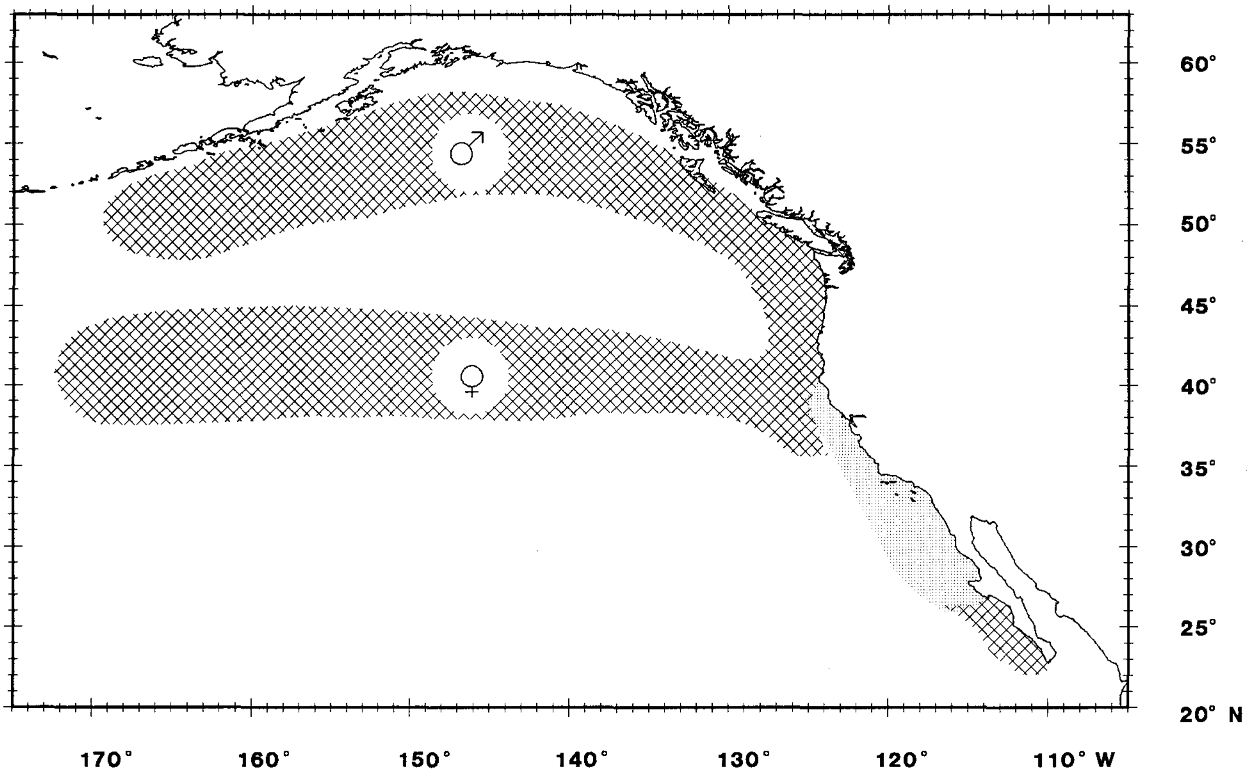

FIG. 4. Distribution of *Mirounga angustirostris* in the northern Hemisphere. Pale shading indicates breeding range; hatching indicates distribution in non-breeding season.

a double keel creating a ventral groove. Scapular morphology is quite variable. Bone density is low, presumably a secondary adaptation associated with deep diving by northern elephant seals (Stein, 1989). There are usually 8–10 brow vibrissae. One vibrissa is present on each side of the median line of the head halfway between the nostril and eye. The mystacial bristles are arranged in seven rows and number from 46 to 49 (Davidson, 1929). The gross anatomy of the cerebrum, cerebellum, and cranial nerves indicate neurological specialization for vision, audition, and facial-axial somatic sensation whereas olfaction appears to be a minor sense; the occipital and parietal lobes of the brain are elaborate and the olfactory bulbs are small (Shipley et al., 1983). Brain mass is about 700 g for adult males and about 640 g for adult females (Shipley et al., 1983).

The pelage of adult males is generally darker brown and sparser than that of females. Growth of a male's nose accelerates during puberty and becomes quite elongated by physical maturity. In addition, the skin on a male's neck and chest becomes thickly calloused and rugose and loses most of its hair. When seals molt they shed the cornified epidermis and old hair in large patches. Young undernourished seals often lose single hairs at some seasons, becoming bald in spots.

Northern elephant seals fast continually for 1 (females) to 3 (males) months while ashore during the reproductive season (December to March) and for 3–4 weeks when molting (April to August; Stewart, 1989). During these fasts, water loss is less than or equal to metabolic water production from metabolization of fat (Ortiz et al., 1978). Respiratory water loss accounts for about 65% of metabolic water production while the remainder is lost as urine, feces, and cutaneous evaporation (Costa and Ortiz, 1980). Complex turbinate processes in the nasal passages function as countercurrent heat exchangers that significantly reduce respiratory water loss to maintain positive water balance (Huntley et al., 1984). In weaned young the total surface area of both turbinate structures is around 720 cm^2 whereas it is around 3,140 cm^2 in adult males (Huntley et al., 1984). Respiratory water recovery is about 72% at an ambient temperature of about 14°C, but the efficiency of the system decreases with a rise in ambient temperature (Huntley et al., 1984). The skin and blubber layer are effective insulators, whereas the appendages, especially the rear flippers, dissipate or conserve heat when blood flow is increased (vasodilation) or decreased (vasoconstriction) to them when ambient temperatures are high and winds are light or when temperatures are low and winds strong, respectively (McGinnis, 1975).

Average rectal temperatures of adult males are between 33–35°C at night and between 35–38°C during the day (Bartholomew, 1954). McGinnis and Southworth (1967, 1971), found that most northern elephant seals were relatively stenothermic but that some were eurythermic and exhibited declines in body temperature when they were inactive while ashore, perhaps due to an abnormal metabolic rate resulting, partially, from malnutrition. Rectal temperatures of fasting, weaned young varies from 35 to 37.4°C (McGinnis, 1975).

When sleeping ashore, northern elephant seals often are apneic, during which bradycardia occurs and metabolism decreases (Bartholomew, 1954; Huntley, 1984). Sleep apneas of up to 21 min have been observed in lactating females (Le Boeuf et al., 1986). The metabolism of fasting, weaned pups is reduced by 48% during periodic sleep apneas (Huntley, 1984). Bartholomew (1954) found no difference in the mean pulse rate of newborn during apnea (ca. 100 beats/min) and eupnea (ca. 99 beats/min) although in older animals (that is, larger than 2.6 m in length) the mean pulse rate during apnea (54 beats/min) was about 15% lower than during eupnea (64.5 beats/min).

During simulated dives in the laboratory, anesthetized elephant seals developed bradycardia on immersion and the heart rate became progressively slower as the duration of the dive increased; after about 40 min of submersion, the heart rate had dropped to about 4 beats/min (Elsner et al., 1966; Hammond et al., 1969; Van Citters et al., 1965). Aortic blood pressure was, however, maintained or slightly elevated suggesting selective vasoconstriction during those simulated dives; blood-flow in the carotid artery decreased as a function of bradycardia, whereas iliac artery blood-flow ceased in simulated dives greater than 10 min (Van Citters et al., 1965).

Blood volume is at least 12% (Elsner et al., 1964) and perhaps as great as 20% of body mass (Simpson et al., 1970). At rest, blood pressure is 120 systolic/90 diastolic (Van Citters et al., 1966). Northern elephant seals have high hematocrit, high blood viscosity (primarily because of high hematocrit), and high plasma viscosity (because of high concentrations of plasma proteins) resulting in increased oxygen storage capacity (Hedrick and Duffield, 1991; Hedrick et al., 1986). Concentrations of hemoglobin were about 19 g/100 ml blood and ca. 22.1 g/100 ml blood in a captive and two wild northern elephant seals, respectively (Lenfant, 1969). Hematocrit increases in young during sleep apneas (Castellini et al., 1986). In yearlings, hemoglobin concentrations are 24.9 g/100 ml, hematocrit is 65.3%, and viscosity for whole blood is 8.9 ± 0.5 cP (Hedrick et al., 1986). Hematocrits of captive northern elephant seals were similar to free-ranging northern elephant seals but white blood cell counts were 41% higher, mean corpuscular volume 12% higher, and total plasma protein levels 16% lower than in wild seals (Wickham et al., 1990). The volume of the inferior vena cava of adults is large and may contain ca. 20% of the total blood volume (Elsner et al., 1964).

During the ca. 28 days that young suckle their body mass increases from approximately 42–127 kg, solely from ingesting milk (Le Boeuf and Ortiz, 1977; Ortiz et al., 1978; Rea and Costa, 1992). During lactation, the milk becomes progressively more concentrated as the fat content rises from about 15 to 55% and the water content declines from ca. 75 to 35%, about 21 days after birth (Le Boeuf and Ortiz, 1977; Riedman and Ortiz, 1979). The protein content remains relatively constant from about 5 to 12% by mass (Riedman and Ortiz, 1979). About 75% of the milk fatty acids are unsaturated and the carbon chain lengths of most are from 14 to 22 (Riedman and Ortiz, 1979).

During the nursing period, young gain ca. 10% while females lose about 4% of their respective body mass/day (Costa et al., 1986); a female transfers an average of 138 kg of milk, equivalent to about 6.0×10^5 kcal of energy, to her young during this period (Ortiz et al., 1984). The metabolic rate of suckling young is higher than that of weaned young (Heath, 1975; Heath et al., 1977) and frequent suckling during the day and at night may permit the maintenance of a high metabolic rate until an insulative subcutaneous fat layer is deposited (Heath et al., 1977). By the time the young seal is weaned, its mother has lost about 42% of her initial body mass, 55% of which is transferred to the young (Costa et al., 1986). A nursing female loses about 15% of her lean body mass compared to about 58% of her adipose mass (Costa et al., 1986). Milk production accounts for about 60% of the female's total daily expenditure of about 163 MJ (Costa et al., 1986).

Body fat of young increases from 4% of body mass at birth to about 48% at weaning when body water constitutes about 40% of total body mass (Ortiz et al., 1978; Rea and Costa, 1992). Once young are weaned they remain ashore and fast for another 6–8 weeks while they molt (Reiter et al., 1978; Stewart and Yochem, 1984). Fasting young lose mass at an average rate of ca. 5 g/kg/day, although the water turnover rate is small (about 13 ml/day) and the average metabolic rate is about 168 kcal/kg$^{3/4}$/day (Ortiz et al., 1978); the proportion of body fat to body mass remains constant during the fast (Rea and Costa, 1992). Fasting young loses ca. 20% of their mass (mean mass loss averages 768 ± 342 g/day; Condit and Ortiz, 1987), but a positive water balance is maintained. Low urine output (<200 ml/day) by fasting young results from tubular resorption rather than depressed glomerular filtration rate (GFR = 78.9–135.2 mL/min; Pernia et al., 1989). Plasma volume decreases with age but there is relatively no change in the ratio of blood volume to mass (Huntley, 1984). Fat is the primary energy substrate during the fast, and protein catabolism is relatively unimportant (Castellini et al., 1987; Condit and Ortiz, 1987; Pernia et al., 1980). Levels of circulating serum glucose, urea nitrogen, and creatinine decline while total protein, albumin and globulin levels remain relatively constant as the fast progresses. Alkaline phosphatase activity increases, serum glutamic oxalacetic transaminase and lactate dehydrogenase remain relatively constant, and electrolyte levels are maintained within a small range during the fast. Although levels of triglycerides, cholesterol, uric acid and bilirubin vary, there are no well-defined trends (Costa and Ortiz, 1982). Weaned young have a glucose mass of ca. 60 mg/kg and a blood glucose concentration of about 174 mg/100 ml. While young fast, ca. 30 g of glucose are removed from the blood each day but only about 25% of it is oxidized, most being recycled and returned to the blood (Keith and Ortiz, 1989). Male northern elephant seals weigh as much as 2,300 kg early in the breeding season (Deutsch et al., 1990). They lose between 4.6 and 7.1 kg each day depending on their age and initial body mass and weigh between 600 kg (subadults) and 1,500 kg (adults) after fasting for 30–90 days (Deutsch et al., 1990; Stewart and DeLong, unpubl. data).

Helm (1983) found that the length of the small intestines of weaned young varied from 2,918 to 5,392 cm, depending on the length of the young, while the large intestine was between 43 and 60 cm long.

Phencyclidine HCl (Sernylan), Ketamine hydrochloride, Sernylan with Sparine and Xylocaine, and Telazol have been used to chemically immobilize northern elephant seals (Antonelis et al., 1987; Briggs et al., 1975; DeLong and Stewart, 1991; Elsner et al., 1966; Stewart, unpubl. data; Van Citters et al., 1965). Doses of 1 mg of Sernylan/kg of body mass produced evidence of lethargy in about 10 min and immobility in 20 min and spontaneous movements usually recurred after 2 h, and within 4 h most animals were ambulatory (Van Citters et al., 1965). Intramuscular injections of Ketamine hydrochloride in doses from 1.4 to 6.9 mg/kg of body mass immobilized adult males, females, and pups within 2–15 min of injection (Antonelis et al., 1987; Briggs et al., 1975; DeLong and Stewart, 1991); the time between induction of immobilization and recovery was dose-related. Briggs et al. (1975) reported a slight increase in heart rate (to about 13 beats/min) in females and a stable body temperature of about 37°C while seals were immobilized. Doses of Ketamine of 2.51–3.50 mg/kg of body mass effectively immobilized juvenile and adult males and females 210–280 cm long; the optimal dose for males >250 cm long was between 2.5–3.0 mg/kg (Antonelis et al., 1987; DeLong and Stewart, 1991). Ketamine induced apnea in about 24% of seals immobilized.

Blubber oils of northern elephant seals are mostly (80%) unsaturated C_{14}–C_{24} fatty acids and smaller amounts (20%) of saturated C_{14}–C_{22} fatty acids (Tsuyuki, 1957, 1958). Blubber of northern elephant seals contains a greater percentage of unsaturated C_{18} fatty acids and a lower percentage of unsaturated C_{20} fatty acids than blubber from southern elephant seals (Tsuyuki and Itoh, 1966). Bryden and Stokes (1969), however, found different fatty acid components of southern elephant seals than those reported by Tsuyuki and Itoh (1966) and suggested that the analyses of fatty acids of northern elephant seals may have suffered from methodological problems.

The eye is protected by a well-developed nictitating membrane with a cartilaginous support along the leading edge that evidently functions to quickly clear the eyes of sand and debris when northern elephant seals are ashore (Morejohn and Briggs, 1973). The eye lens is large and spherical to compensate for the absence of the refractive power of the cornea in water which permits enough accommodation to form a well-defined image on the retina (Walls, 1963). The retina has a high ratio of receptor to ganglion cells, relative to that of other pinnipeds, suggesting that its sensitivity to light is greater than in other species (Landau and Dawson, 1970).

Swimming, as in other phocids, mimics that of thunniform propulsors (Fish et al., 1988); locomotion occurs by alternate sweeps of the hindflippers while the fore-flippers are adducted against the sides and the neck is retracted. While both hindflippers are swept laterally, the digits of the trailing flipper are spread while the digits of the leading flipper are closed.

ONTOGENY AND REPRODUCTION. A female northern elephant seal gives birth to one young about 6 days after hauling out between December and March and nurses it for about 27 days before abruptly weaning it when she mates and returns to sea to feed for 2 months (Le Boeuf et al., 1972; Reiter et al., 1978; Stewart, 1989; Stewart and Yochem, 1984). Full gestation is about 11 months but a 2–3 month delay in attachment of the fertilized egg to the uterine wall (delayed implantation), similar to other pinnipeds, is presumed. Twins have never been observed. Premature births are rare (Huber, 1987; Stewart, 1989). The sex ratio at birth and at weaning rarely varies from parity (Le Boeuf et al., 1989*a*; Stewart, 1989). At birth young are about 125 cm (standard length) and weigh about 35 kg. The black natal pelage is molted shortly after weaning at 3–4 weeks of age and is replaced by a silvery-gray pelage. This hair gradually fades to a dark brown dorsally and tan ventrally before pups go to sea at 11–16 weeks of age. Most females nurse their own pups exclusively until weaned, although the number of orphaned and adopted pups is influenced by the timing and severity of winter storms and, perhaps, by crowding on rookeries (Huber, 1987; Le Boeuf, 1972; Riedman and Le Boeuf, 1982).

Preweaning mortality varies among rookeries from about 3–4% at San Nicolas Island (Odell, 1974; Stewart, 1989; Stewart and Yochem, 1984, 1991), 5–10% on Isla de Guadalupe (Bartholomew, 1952) and San Miguel Island (Stewart, 1989, 1992), 13–48% on Año Nuevo Island (Le Boeuf and Briggs, 1977; Le Boeuf et al., 1972; Riedman and Le Boeuf, 1982), and 7–76% on South Farallon Islands (Huber et al., 1991*b*). Reiter et al. (1981) reported that neonatal mortality was density-dependent on Año Nuevo Island but Stewart (1989) found no significant density-dependent relationship there or on San Miguel, San Nicolas, or South Farallon Islands; preweaning survival of pups may be primarily habitat-dependent (Stewart, 1989). Most neonate deaths result from separation of mothers and young during the first week of life and subsequent starvation of young (Le Boeuf and Briggs, 1977; Le Boeuf et al., 1972; Morejohn and Briggs, 1973; Stewart, 1989).

Reiter et al. (1978) estimated that at least 50% of young survive from about 3 to 7 months of age and found that there was no difference in survival between males and females to 2 years of age. From tagged cohorts born on the Farallon Islands, Huber et al. (1991*b*) estimated that from 1978 through 1982, minimum survival of tagged young was 45% to September, and 35, 30, and 22% to 1, 2, and 3 years of age, respectively. However, survival of the 1983 and 1984 cohorts was significantly lower, ca. 15, 8, and 2%, to 1, 2, and 3 years of age, respectively. Further, age-specific natality among 3–10 year-olds was lower in 1984 and 1985 than in other years, apparently related to poor feeding conditions during El Niño-Southern Oscillation event of 1982–1983 (Huber et al., 1991*a*, 1991*b*).

Females give birth when 2 years old on occasion (Reiter et al., 1981; Stewart, unpubl. data). At South Farallon Islands between 1975 and 1989 age at primiparity ranged from 3 to 8 years but most (62.6%) females first gave birth when 4 years old (Huber, 1987; Sydeman et al., 1991). At Año Nuevo Island, Reiter et al. (1981) found that 1, 20, 62, 8, and 1% of the females studied there first gave birth when 2, 3, 4, 5, and 6 years of age, respectively. Reiter et al. (1981) and Le Boeuf et al. (1972) reported that once a female gave birth, she gave birth every year afterwards until death. Huber (1987), however, found that 8–20% of females that gave birth in any year did not give birth the following year. The range in ages of females giving birth on South Farallon Islands increased gradually from 3–5 years in 1975 to 4–13 years in 1983 (Huber, 1987). Huber et al. (1991*b*) found that age-specific natality of females at South Farallon Islands was 0.13 for 3-year-olds, 0.75 for 4-year-olds, and 0.80 for 5- to 10-year-olds. The success of females in weaning their young increased with age and previous maternal experience at South Farallon Islands between 1978 and 1989 (Sydeman et al., 1991). Lifetime reproductive success of females at Año Nuevo Island was about 0.75 young (Le Boeuf and Reiter, 1987).

Males may be sexually mature when 6 or 7 years old, but generally do not breed until 9 or 10 years old, except at newly established rookeries (Le Boeuf et al., 1974). During the breeding season (December to March) males compete with each other for access to estrous females and dominance hierarchies are consequently established. Males spend <1% of their time in aggressive activities and most agonistic interactions are visual and vocal threats rather than physical combat (Cox, 1981). Fewer than one-third of males present during the breeding season may copulate and even fewer account for most of the copulations (Le Boeuf, 1974; Le Boeuf and Peterson, 1969*a*).

ECOLOGY. Great white sharks (*Carcharodon carcharias*) and killer whales (*Orcinus orca*) prey occasionally on northern elephant seals (Ainley et al., 1981, 1985; Le Boeuf et al., 1982; Rice, 1968; Stewart and Yochem, 1985) but they evidently have no significant impact on demography of elephant seals. Small numbers of northern elephant seals become entangled in fishing lines, net fragments, and marine debris but the population effects of any associated mortality are unpredictable (Stewart and Yochem, 1987).

There are three seasonal peaks in abundance; one in late January, at the height of the breeding season; one in late April and early May when adult females and juveniles are ashore molting; and one in October when non-pregnant females, pups-of-the-year, yearlings, and juveniles haul out briefly (Bartholomew, 1951; Bartholomew and Boolootian, 1960; Bartholomew and Hubbs, 1952, 1960; Odell, 1974, 1977; Stewart, 1989; Stewart and Yochem, 1984). Relatively few seals are ashore in June, when subadult males molt, and in July and August when adult males molt.

Females return to land to molt in April and May about 65–85 days after departing at the end of the breeding season in January and February (Huber et al., 1991*a*; Le Boeuf et al., 1986; Stewart and DeLong, in press *a*, in press *b*; Stewart and Yochem, 1991). Females that successfully wean their young spend more time at sea than do unsuccessful females (Stewart and Yochem, 1984). In 1983 females spent substantially more time at sea before returning to molt than in other years and the differences were attributed to the anomalous oceanographic conditions associated with the 1982/1983 El Niño southern Oscillation (Huber et al., 1991*a*; Stewart, 1989; Stewart and Yochem, 1991). Females spend about 4 weeks ashore in April and May while molting and then return to sea where they remain feeding until December or January (Stewart and DeLong, in press *b*); some non-pregnant females haul out briefly in autumn (Huber, 1987).

Examination of stomach contents of northern elephant seals found ashore dead during various seasons indicated that they had eaten rockfish (*Sebastes* sp.), ratfish (*Hydrolagus colliei*), spiny dogfish (*Squalus acanthis*), squid (several genera), skate (*Raja* sp.), spotted cusk eel (*Otophidium taylori*), plainfin midshipman (*Poricthyes notatus*), flatfish (several species), catshark (*Apristurus brunneus*), octopus (*Octopus* sp.), Pacific lamprey (*Lampetra tridentata*), hagfish (*Epatretus* sp.), Pacific whiting (*Merluccius productus*), and stingray (*Urolophus halleri*; Antonelis and Fiscus, 1980; Condit and Le Boeuf, 1984; Cowan and Guiguet, 1956; Frieburg and Dumas, 1954; Jones, 1981; Morejohn and Baltz, 1970; Pike and MacAskie, 1969). Recent stomach lavage studies of living seals have shown that stomachs of dead seals did not fully describe the diet of northern elephant seals; they prey mostly on mesopelagic squid and, to a lesser extent, fish (Antonelis et al., 1987, in press; DeLong and Stewart, 1991).

Brown and Norris (1956) observed adult seals feeding, along with Pacific white-sided dolphins (*Lagenorhynchus obliquidens*), on northern anchovies (*Engraulis mordax*) in southern California waters. Condit and Le Boeuf (1984) reported observations of elephant seals eating stingrays (*Urolophus halleri*), dogfish sharks (*Squalus acanthus*), blue sharks (*Prionace glauca*) and angel sharks (*Squatina californica*).

Adult males and females that breed at San Miguel Island forage in different areas; males migrate to the Gulf of Alaska and eastern Aleutian islands from March through early August (post-breeding) and then again from early September until December (post-molt) whereas females remain further south during their post-breeding and post-molt foraging migrations, moving well off the coasts of Oregon and Washington as far west as 173°W longitude (Stewart and DeLong, in press *a*, in press *b*).

Exudative pyodermatitis was present on four northern elephant seals and *Streptococcus* sp., *Bacillus* sp., *Escherichia coli*, and *Acinetobacter* sp. were cultured from those skin lesions and from the peripheral lymph nodes; another yearling seal had poxlike dermo-epidermal lesions covering most of its body (Stroud and Roffe, 1979). An unidentified fungus that causes depigmented lesions on the epidermis, which disappear when the animal molts, has been observed in captive northern elephant seals (Sweeney, 1974).

Goose barnacles, *Lepas pacifica*, *L. anatifera*, and *L. hilli*, and stalked barnacles, *Conchoderma auritum* and *C. virgatum*, occasionally attach to the skin of young northern elephant seals (Baldridge, 1977; Joseph et al., 1986; Roletto and Van Syoc, 1986). The greenish colored alga *Navicula grevillei* also is occasionally found on the dorsal surface of young elephant seals (Baldridge, 1977). The cookie cutter shark (*Isistius*) evidently attaches to the skin of some seals and may remove small plugs of their skin and blubber (Le Boeuf et al., 1987).

Several serotypes of San Miguel Sea Lion Virus, a marine calicivirus, were isolated from northern elephant seals on San Miguel Island (Barlough et al., 1986, 1987) but antibodies to Tillamook (bovine) caliciviruses were not found in sera collected from 66 seals there (Barlough et al., 1987).

Three species of nematodes (*Anasakis simplex—A. similis*, *Terranova* (*Porrocaecum*) *decipiens*, *Contracaecum osculatum*) have been found in stomachs of elephant seals (Dailey, 1975; Dailey and Brownell, 1972; Stroud and Dailey, 1978). Stroud and Dailey (1978) observed gastric ulcers associated with large numbers of the nematodes *C. osculatum* and *A. simplex*. The trematodes *Cryptocotyle lingua* and *Pricetrema zalophi* have been isolated from intestines, the trematode *Zalphotrema hepaticum* from the liver, and the nematodes *Parafilaroides* sp. and *Ostostrongylus circumlitus* have been found in the lungs (Dailey and Brownell, 1972; Stroud and Dailey, 1978; Sweeney, 1974). The turbinates are frequently infested by the nasal mites *Halarchne miroungae* (Ferris, 1925). The acanthocephalans *Corynosoma bullosum* and *Corynosoma* sp. have also been found (Dailey, 1975; Dailey and Brownell, 1972).

Stroud and Roffe (1979) observed verminous pneumonia in one yearling that was heavily infested with lungworm (*Parafilaroides* sp.) and in another that was infested with *O. circumlitus*. Saunders and Hubbard (1966) described emphysema as a cause of death among captive seals.

BEHAVIOR. As males compete for access to estrous females during the breeding season, dominance hierarchies are established through stereotyped visual and vocal threats and, occasionally, physical combat (Bartholomew, 1952; Le Boeuf and Peterson, 1969*a*; Shipley et al., 1981, 1986).

Vocal threats include the snort, made by expulsion of air through the proboscis, and the clap-threat, the primary vocal threat so-called because "it is an extremely loud, resonant, clapping sound with a metallic quality which suggests the exhaust noise made by a diesel engine" (Bartholomew, 1952; Bartholomew and Collias 1962:11). Bartholomew and Collias (1962), Le Boeuf and Peterson (1969*b*) and Shipley et al. (1981) described differences among individuals in the pulse or syllable (Shipley et al., 1986:527) rates in clap-threats. Further, Bartholomew and Collias (1962), Sandegren (1976), and Shipley et al. (1981, 1986) suggested that characteristics of clap-threat vocalizations might communicate identity, size, age, or dominance status to other males. Le Boeuf and Peterson (1969*b*) reported differences in syllable rates among rookeries on San Nicolas, San Miguel, and Año Nuevo islands, but Le Boeuf and Petrinovich (1974*a*, 1975) later found that the syllable rates varied among years on Año Nuevo Island. Shipley et al. (1981) found no evidence of dialects among northern elephant seal bulls. Clap-threats are of several types (clap, clap burst, and patterned; Shipley et al. 1986) and have different syllable rates which vary with age. The syllable rates of young bulls are greater than those of adults; the syllable rates of young juvenile males vary greatly, but stabilize as they mature (Shipley et al., 1981, 1986). The syllable rates of northern elephant seal bulls that emit clap-threats are faster than those of bulls that emit clap bursts. Dominant and subordinate males are least active vocally at mid-day, perhaps because of thermoregulatory constraints (Shipley and Strecker, 1986).

Northern elephant seals create low-frequency, substrate-borne sounds incidental to locomotion and air-borne vocalizations and conspecifics detect and alert to those seismic disturbances. Those seismic signals appear to be important social cues that help seals, particularly adult males, maintain social hierarchies in crowded, busy and noisy environments (especially at night), and help minimize energy expenditure during the breeding-season fasts (Shipley et al., in press).

Nursing young produce two basic vocalizations when distressed, uncomfortable, or to attract or prod their mothers to permit them to suckle (Bartholomew and Collias, 1962). Females respond to vocalizations of their young with an unpulsed attraction call, whereas they produce a highly pulsed, harsh call when threatening other females, males, or alien young (Bartholomew and Collias, 1962). Klopfer and Gilbert (1966) believed that females could discriminate between vocalizations of their own and alien young and Petrinovich (1974) found that females responded more frequently to distress calls of their own pups than to those of alien young.

Dominance is determined by ritualized threat displays and, to a lesser extent, fighting, and the hierarchy is structured according to age, size, and previous breeding experiences of males (Sandegren, 1976). Older, higher-ranking males have greater reproductive success than lower-ranking males, because dominance permits them greater access to estrous females (Le Boeuf, 1971; Le Boeuf and Peterson, 1969*a*). Most males never breed (Le Boeuf, 1974). A few subordinate males may breed each year, but their reproductive success is low (Cox, 1983). Christenson (1974) and Christenson and Le Boeuf (1978) found that aggressive females at Año Nuevo Island were more likely to wean their pups because their young were bitten less often than were those of submissive females. Ribic (1988), however, found that female aggression on South Farallon Islands was stimulated by presence of the young, but that weaning a pup successfully was influenced more by dominance rank than by aggression, which she found to be mostly independent of rearing success. Reiter et al. (1981) reported that females more than 5 years old were more likely to wean their pups than were younger females.

Female southern elephant seals (*M. leonina*) are less aggressive than female northern elephant seals, resulting in fewer mother–young separations and lower young mortality (Le Boeuf and Petrinovich 1974*b*). The differences in aggression are, however, related to lesser crowding on rookeries of the southern elephant seal.

Rasa (1971) described the predominant social behavior among weaned male young as wrestling, similar to the adult male dominance fights, and the predominant behavior among weaned female young as a vocalization that served to maintain or increase spacing among seals. Young are most active in morning and evening and least active at mid-day (Rasa, 1971; Reiter et al., 1978). Suckling young are dependent on their mothers for protection and most pre-weaning mortality occurs because of separation of cows and their young that may lead to starvation and death or to fatal bites from alien females. Sandflipping behavior (tossing sand on the back with the fore-flippers) is both a thermoregulatory response to overheating (McGinnis, 1975; White and Odell, 1971) and a displacement behavior when seals are agitated or stressed (Heath and Schusterman, 1975).

When at sea adult male and female northern elephant seals dive continually with rare interruption. Dives average ca. 23 min long (Le Boeuf et al., 1988, 1989*b*; DeLong and Stewart, 1991; Stewart and DeLong, in press *a*, in press *b*). The longest recorded dive is 77 min for an adult male (Stewart and DeLong, 1990). Inter-dive breathing intervals at the surface are brief, lasting 2–4 min and inter-dive surface periods longer than 5 min occur only rarely during the seals' 3–8 months at sea (Le Boeuf et al., 1989*b*; Stewart and DeLong, in press *a*, in press *b*).

Maximum depths of dives average between 350 and 550 m but there is substantial variation depending on time of day and season (Le Boeuf et al., 1989*b*; DeLong and Stewart, 1991; Stewart and DeLong, in press *a*, in press *b*). The deepest recorded dives are 1,585 m for a male and 1,561 m for a female (Stewart and DeLong, 1990).

Adult northern elephant seals make two migrations each year (Stewart and DeLong, in press *a*, in press *b*). In January and February females depart rookeries in southern California and range north to 40–45°N latitude and as far west as 173°W longitude during a 65–75 day foraging period before they return to the southern California Channel Islands in April and May to molt. Females return to sea in late May and June and migrate to the same general areas that they visited in early spring; they remain there for 6–8 months before returning to the islands again to breed in January. Adult males depart rookeries of the Channel Islands in late February and March and spend the next 3–4 months traveling to and foraging in offshore areas in the Gulf of Alaska and near the eastern Aleutian Islands. They return to the Channel Islands by July, haul out for 3–4 weeks while molting and then migrate north to the Gulf of Alaska again before returning to Channel Islands rookeries by December and January.

In spring 1982, two females gained 25 and 132 kg in 66 and 63 days at sea, respectively, whereas two in spring 1983 gained 19 and 57 kg during 127 and 93 days at sea, respectively, and 7 females in spring of 1985 and 1986 each gained about 76 kg, on average, during an average of about 72 days at sea (Le Boeuf et al., 1986, 1988). Adult males gain about 30–40% of their post-breeding season mass while at sea in spring and early summer (Stewart and DeLong, unpubl. data).

GENETICS. The modal chromosome number is 34 (Duffield-Kulu, 1972). Electrophoresis of blood samples from 159 young from five rookeries detected no polymorphisms among 21 blood proteins (Bonnell and Selander, 1974). Further, little variability was detected in hypervariable minisatellite DNA (Lehman et al., in press). Low genetic variability has been hypothesized to have resulted from loss of genic variation during the population bottleneck in the late 1800s when the species was reduced to several hundred or fewer seals.

REMARKS. The geographic derivation of *M. angustirostris* is unknown although two alternate hypotheses have been proposed. Davies (1958) suggested that the northern elephant seal arose from a Southern Hemisphere ancestor that expanded into the North Pacific during the Pleistocene and was later isolated from its parent stock when equatorial waters subsequently warmed. McLaren (1975:45) believed that the entry of elephant seals into the North Pacific was ". . . clearly by way of western South America." Briggs and Morejohn (1976) presented morphological evidence to support the hypothesis that the genus arose in north tropical regions and that the southern elephant seal (*M. leonina*) evolved directly from the northern elephant seal or from a common ancestor.

According to the most recent taxonomic scheme, elephant seals (northern and southern species) are assigned to the tribe Miroungini of the subfamily Monachinae which is in the family Phocidae of the Order Carnivora (de Muizon, 1982). *Mirounga* is derived from *miouroung*, the Australian native name for the elephant seal. *Angustus* (Latin) means narrow and *rostris* means snout, referring to the narrower snout of this species compared to the Southern Hemisphere species, *M. leonina* (King, 1983).

LITERATURE CITED

Ainley, D. G., C. S. Strong, H. R. Huber, T. J. Lewis, and S. Morrell. 1981. Predation by sharks on pinnipeds at the Farallon Islands. United States Fishery Bulletin, 78:941–945.

Ainley, D. G., R. P. Henderson, H. R. Huber, R. J. Boekelheide, S. G. Allen, and T. L. McElroy. 1985. Dynamics of white shark/pinniped interactions in the Gulf of the Farallones. Memoirs of the Southern California Academy of Sciences, 9:109–122.

Allen, J. A. 1880. History of North American pinniped, a monograph of the walruses, sea lions, sea bears, and seals of North America. United States Geological and Geographical Surveys of the Territories, Miscellaneous Publications, 12:1–785.

Allen, S. G., S. C. Peaslee, and H. R. Huber. 1989. Colonization by northern elephant seals of the Point Reyes Peninsula, California. Marine Mammal Science, 5:298–302.

Anonymous. 1939. The northern elephant seal in California. Journal of Mammalogy, 20/21:285–286.

Anthony, A. W. 1924. The elephant seal off Santa Cruz Island, California. Journal of Mammalogy, 2:112–113.

Antonelis, G. A., Jr., and C. H. Fiscus. 1980. The pinnipeds of the California current. California Cooperative Oceanic Fisheries Investigations Reports, 21:68–78.

Antonelis, G. A., Jr., M. S. Lowry, D. P. DeMaster, and C. H. Fiscus. 1987. Assessing northern elephant seal feeding habits by stomach lavage. Marine Mammal Science, 3:308–322.

Antonelis, G. A., M. S. Lowry, C. H. Fiscus, B. S. Stewart, and R. L. DeLong. In press. Diet of the northern elephant seal. *In* Elephant seals (B. J. Le Boeuf and R. M. Laws, eds.). University of California Press, Berkeley.

Baldridge, A. 1977. The barnacle *Lepas pacifica* and the alga *Navicula grevillei* on northern elephant seals, *Mirounga angustirostris.* Journal of Mammalogy, 58:428–429.

Barlough, J. E., E. S. Berry, D. E. Skilling, and A. W. Smith. 1986. Sea lions, caliciviruses and the sea. Avian/Exotic Practice, 3:8–20.

Barlough, J. E., E. S. Berry, A. W. Smith, and D. E. Skilling. 1987. Prevalence and distribution of serum neutralizing antibodies to Tillamook (bovine) caliciviruses in selected populations of marine mammals. Journal of Wildlife Diseases, 23: 45–51.

Barnes, L. G., and E. D. Mitchell. 1975. Late Cenozoic northeast Pacific phocidae. Rapports et Procès-verbaux des Réunions Conseil International Pour L'exploration de la Mer, 169:34–42.

Bartholomew, G. A., Jr. 1950. Reoccupation by the elephant seal of Los Coronados Islands, Baja California. Journal of Mammalogy, 31:98.

———. 1951. Spring, summer, and fall censuses of the pinnipeds on San Nicolas Island, California. Journal of Mammalogy, 32: 15–21.

———. 1952. Reproductive and social behavior of the northern elephant seal. University of California Publications in Zoology, 47:369–472.

———. 1954. Body temperature and respiratory and heart rates in the northern elephant seal. Journal of Mammalogy, 35:211–218.

Bartholomew, G. A., and R. A. Boolootian. 1960. Numbers and population structure of the pinnipeds on the California Channel Islands. Journal of Mammalogy, 41:366–375.

Bartholomew, G. A., and N. E. Collias. 1962. The role of vocalization in the social behavior of the northern elephant seal. Animal Behavior, 10:7–14.

Bartholomew, G. A., and C. L. Hubbs. 1952. Winter population of pinnipeds about Guadalupe, San Benito, and Cedros Islands, Baja California. Journal of Mammalogy, 33:160–171.

———. 1960. Population growth and seasonal movements of the northern elephant seal, *Mirounga angustirostris.* Mammalia, 24:313–324.

Bonnell, M. L., and R. K. Selander. 1974. Elephant seals: genetic variation and near extinction. Science, 184:908–909.

Bonnot, P., G. H. Clark, and S. R. Hatton. 1938. California sea lion census for 1938. California Fish and Game, 24:415–419.

Briggs, G. D., R. V. Henrickson, and B. J. Le Boeuf. 1975. Ketamine immobilization of northern elephant seals. Journal of the American Veterinary Medical Association, 167:546–548.

Briggs, K. T. 1974. Dentition of the northern elephant seal. Journal of Mammalogy, 55:158–171.

Briggs, K. T., and G. V. Morejohn. 1975. Sexual dimorphism in the mandibles and canine teeth of the northern elephant seal. Journal of Mammalogy, 56:224–231.

———. 1976. Dentition, cranial morphology, and evolution in elephant seals. Mammalia, 40:199–222.

Brown, D. H., and K. S. Norris. 1956. Observations on captive and wild cetaceans. Journal of Mammalogy, 37:311–326.

Bryden, M. M., and G. B. Stokes. 1969. Metabolism of fatty acids in the southern elephant seal, *Mirounga leonina.* Canadian Journal of Biochemistry, 47:757–760.

Castellini, M. A., D. P. Costa, and A. C. Huntley. 1986. Hematocrit variation during sleep apnea in elephant seal pups. American Journal of Physiology, 251:R429–R431.

———. 1987. Fatty acid metabolism in fasting elephant seal pups. Journal of Comparative Physiology, 157B:445–448.

Christenson, T. E. 1974. Aggressive and maternal behaviors of the female northern elephant seal. Ph.D. dissert., University of California, Berkeley, 69 pp.

Christenson, T. E., and B. J. Le Boeuf. 1978. Aggression in the female northern elephant seal, *Mirounga angustirostris.* Behaviour, 64:158–171.

Condit, R., and B. J. Le Boeuf. 1984. Feeding habits and feeding grounds of the northern elephant seal. Journal of Mammalogy, 65:281–290.

Condit, R. S., and C. L. Ortiz. 1987. The physiological transition from fasting to feeding in weaned elephant seal pups. Marine Mammal Science, 3:207–219.

Cooper, C. F., and B. S. Stewart. 1983. Demography of northern elephant seals, 1911–1982. Science, 219:969–971.

Costa, D. P., B. J. Le Boeuf, A. C. Huntley, and C. L. Ortiz. 1986. The energetics of lactation in the northern elephant seal. Journal of Zoology, 209:21–33.

Costa, D. P., and C. L. Ortiz. 1980. Water, electrolyte and nitrogen balance in fasting weaned elephant seal pups, *Mirounga angustirostris.* The Physiologist, 23:98.

———. 1982. Blood chemistry homeostasis during prolonged fasting in the northern elephant seal. American Journal of Physiology, 242:R591–R595.

Cowan, I. M., and S. G. Carl. 1945. The northern elephant seal (*Mirounga angustirostris*) in British Columbia waters and vicinity. The Canadian Field-Naturalist, 59:170–171.

Cowan, I. M., and C. J. Guiguet. 1956. The mammals of British Columbia. British Columbia Provincial Museum Handbook, 11: 1–251.

Cox, C. R. 1981. Agonistic encounters among male elephant seals: frequency, context and the role of female preference. American Zoologist, 21:197–209.

———. 1983. Reproductive behavior of subadult elephant seals: the cost of breeding. Pp. 89–115, *in* Behavioral energetics: the cost of survival in vertebrates (W. P. Aspey and S. I. Lustick, eds.). Ohio State University Press, Columbus, 300 pp.

Dailey, M. D. 1975. The distribution and intraspecific variation of helminth parasites in pinnipeds. Rapports et Procès-verbaux des Réunions Conseil International Pour L'exploration de la Mer, 169:338–352.

Dailey, M. D., and R. L. Brownell, Jr. 1972. A checklist of marine mammal parasites. Pp. 528–589, *in* Mammals of the sea: biology and medicine (S. H. Ridgway, ed.). Charles C Thomas, Springfield, Illinois, 812 pp.

Davidson, M. E. M. 1929. Notes on the northern elephant seal. Proceedings of the California Academy of Sciences, 18:229–243.

Davies, J. L. 1958. The pinnipedia: an essay in zoogeography. Geographical Review, 48:474–493.

DeLong, R. L., and B. S. Stewart. 1991. Diving patterns of northern elephant seal bulls. Marine Mammal Science, 7:369–384.

DeLong, R. L., B. S. Stewart, and R. D. Hill. 1992. Documenting migrations of northern elephant seals using daylength. Marine Mammal Science, 8:155–159.

de Muizon, C. 1982. Phocid phylogeny and dispersal. Annals of the South African Museum, 89:175–213.

de Muizon, C., and Q. B. Hendey. 1980. Late tertiary seals of the South Atlantic Ocean. Annals of the South African Museum, 82:91–128.

Deutsch, C. J., M. P. Haley, and B. J. Le Boeuf. 1990. Reproductive effort of male northern elephant seals: estimates from mass loss. Canadian Journal of Zoology, 68:2580–2593.

Duffield-Kulu, D. 1972. Evolution and cytogenetics. Pp. 503–527, *in* Mammals of the sea: biology and medicine (S. H. Ridgway, ed.). Charles C Thomas, Springfield, Illinois, 812 pp.

Elliot, D. G. 1904. Pinnipedia. Part 2. Pp. 538–546, *in* The land and sea mammals of middle America and the West Indies. Field Museum of Natural History, Zoology Series, 4, 685 pp.

Elsner, R., D. L. Franklin, R. L. Van Citters, and D. W. Kenny. 1966. Cardiovascular defense against asphyxia. Science, 153: 944–949.

Elsner, R. W., P. F. Scholander, A. B. Craig, E. G. Diamond, L. Irving, M. Pilson, K. Johanson, and E. Bradstreet. 1964. Venous oxygen reservoir in the diving elephant seal. The Physiologist, 7:124.

Ferris, G. F. 1925. On two species of the genus *Halarchne* (Acarina; Gamasidae). Parasitology, 17:163–167.

Fish, F. E., S. Innes, and K. Ronald. 1988. Kinematics and estimated thrust production of swimming harp and ringed seals. Journal of Experimental Biology, 137:157–173.

Flower, W. H. 1881. On the elephant seal *Macrorhinus leoninas* Linn. Proceedings of the Zoological Society of London, 1881(10): 145–162.

Freiberg, R. E., and P. C. Dumas. 1954. The elephant seal (*Mirounga angustirostris*) in Oregon. Journal of Mammalogy, 35:129.

Gill, T. 1866*a*. Prodome of a monograph of the pinnipedes. Proceedings of the Essex Institute, Salem Communications, 5:3–13.

———. 1866*b*. On a new species of the genus *Macrorhinus*. Proceedings of the Chicago Academy of Sciences, 1:33–34.

Gray, J. E. 1871. Supplement to the catalogue of seals and whales in the British Museum. London, British Museum. 103 pp.

Hammond, D. D., R. Elsner, G. Simison, and R. Hubbard. 1969. Submersion bradycardia in the newborn elephant seal, *Mirounga angustirostris*. American Journal of Physiology, 216: 220–222.

Heath, M. E. 1975. Aspects of thermoregulation in weaned northern elephant seal pups. M.S. thesis, California State University, Hayward, 87 pp.

Heath, M. E., and R. J. Schusterman. 1975. "Displacement" sand flipping in the northern elephant seal, *Mirounga angustirostris*. Behavioral Biology, 14:379–385.

Heath, M. E., S. M. McGinnis, and D. Alcorn. 1977. Comparative thermoregulation of suckling and weaned pups of the northern elephant seal, *Mirounga angustirostris*. Comparative Biochemistry and Physiology, 57A:203–206.

Hedrick, M. S., and D. A. Duffield. 1991. Haematological and rheological characteristics of blood in seven marine mammal species: physiological implications for diving behaviour. Journal of Zoology (London), 225:273–283.

Hedrick, M. S., D. A. Duffield, and L. H. Cornell. 1986. Blood viscosity and optimal hematocrit in a deep-diving mammal, the northern elephant seal (*Mirounga angustirostris*). Canadian Journal of Zoology, 64:2081–2085.

Helm, R. C. 1983. Intestinal length of three California pinniped species. Journal of Zoology (London), 199:207–304.

Hendey, Q. B. 1972. The evolution and dispersal of the monachinae. Annals of the South African Museum, 59:99–113.

Huber, H. R. 1987. Natality and weaning success in relation to age of first reproduction in northern elephant seals. Canadian Journal of Zoology, 65:1311–1316.

Huber, H. R., C. Beckham, and J. Nisbet. 1991*a*. Effects of the 1982–83 El Niño on northern elephant seals at the South Farallon Islands, California. Pp. 219–233, *in* Pinnipeds and El Niño: responses to environmental stress (F. Trillmich and K. Ono, eds.). Springer-Verlag, Berlin, 293 pp.

Huber, H. R., A. C. Rovetta, L. A. Fry, and S. L. Johnston. 1991*b*. Age-specific natality in the northern elephant seal on the South Farallon Islands, California. Journal of Mammalogy, 72:525–534.

Huntley, A. C. 1984. Relationships between metabolism, respiration, heart rate, and arousal states in the northern elephant seal. Ph.D. dissert., University of California, Santa Cruz, 89 pp.

Huntley, A. C., D. P. Costa, and R. D. Rubin. 1984. The contribution of nasal countercurrent heat exchange to water balance in the northern elephant seal. Journal of Experimental Biology, 113:447–454.

Jones, R. E. 1981. Food habits of smaller marine mammals from northern California. Proceedings of the California Academy of Sciences, 42:409–433.

Joseph, B. E., L. H. Cornell, and K. G. Osborn. 1986. Occurrence of ectoparasitic barnacles on northern elephant seals (*Mirounga angustirostris*). Journal of Mammalogy, 67:772.

Keith, E. O., and C. L. Ortiz. 1989. Glucose kinetics in neonatal elephant seals during postweaning aphagia. Marine Mammal Science, 5:99–115.

King, J. E. 1966. Relationships of the hooded and elephant seals (genera *Cystophora* and *Mirounga*). Journal of Zoology (London), 148:385–398.

———. 1972. Observations on phocid skulls. Pp. 81–115, *in* Functional anatomy of marine mammals (R. J. Harrison, ed.). Academic Press, New York, 451 pp.

———. 1983. Seals of the world. Second ed. Comstock Publishing Associates, Ithaca, New York, 240 pp.

King, J. E., A. K. Fukuyama, S. J. Krenn, and A. S. Setran. 1989. New mainland haul-out site for the northern elephant seal, *Mirounga angustirostris*, in Central California. California Fish and Game, 75:244–247.

Kiyota, M., N. Baba, and M. Mouri. 1992. Occurrence of an elephant seal in Japan. Marine Mammal Science, 8:433.

Klopfer, P. H., and B. K. Gilbert. 1966. A note on retrieval and recognition of young in the elephant seal, *Mirounga angustirostris*. Zeitschrift Tierpsychologie, 6:757–760.

Kovacs, K. M., and D. M. Lavigne. 1986. Cystophora cristata. Mammalian Species, 258:1–9.

Landau, D., and W. W. Dawson. 1970. The histology of retinas from the pinnipedia. Vision Research, 10:691–702.

Le Boeuf, B. J. 1971. The aggression of the breeding bulls. Natural History, 80:82–94.

———. 1972. Sexual behavior in the northern elephant seal, *Mirounga angustirostris*. Behaviour, 41:1–26.

———. 1974. Male-male competition and reproductive success in elephant seals. American Zoologist, 14:163–176.

Le Boeuf, B. J., and K. T. Briggs. 1977. The cost of living in a seal harem. Mammalia, 41:167–195.

Le Boeuf, B. J., and C. L. Ortiz. 1977. Composition of elephant seal milk. Journal of Mammalogy, 58:683–685.

Le Boeuf, B. J., and K. J. Panken. 1977. Elephant seals breeding on the mainland in California. Proceedings of the California Academy of Sciences, 41:267–280.

Le Boeuf, B. J., and R. S. Peterson. 1969*a*. Social status and mating activity in elephant seals. Science, 163:91–93.

———. 1969*b*. Dialects in elephant seals. Science, 166:1654–1656.

Le Boeuf, B. J., and L. F. Petrinovich. 1974*a*. Dialects of northern elephant seals, *Mirounga angustirostris*: origin and reliability. Animal Behavior, 22:656–663.

———. 1974*b*. Elephant seals: interspecific comparisons of vocal and reproductive behavior. Mammalia, 38:17–32.

———. 1975. Elephant seal dialects: are they reliable? Rapports et Procès-verbaux des Réunions Conseil International Pour L'exploration de la Mer, 169:213–218.

Le Boeuf, B. J., and J. Reiter. 1987. Lifetime reproductive success in northern elephant seals. Pp. 344–362, *in* Reproductive success (T. H. Clutton-Brock, ed.). University of Chicago Press, Chicago, 538 pp.

Le Boeuf, B. J., D. G. Ainley, and T. J. Lewis. 1974. Elephant seals on the Farallones: population structure of an incipient breeding colony. Journal of Mammalogy, 55:370–385.

Le Boeuf, B. J., R. Condit, and J. Reiter. 1989*a*. Parental investment and the secondary sex ratio in northern elephant seals. Behavioral Ecology and Sociobiology, 25:109–117.

Le Boeuf, B. J., J. E. McCosker, and J. Hewitt. 1987. Crater wounds on elephant seals: the cookie cutter shark strikes again. United States Fishery Bulletin, 85:387–392.

Le Boeuf, B. J., M. Riedman, R. S. Keyes. 1982. White shark predation on pinnipeds in California coastal waters. United States Fishery Bulletin, 80:891–895.

Le Boeuf, B. J., R. J. Whiting, and R. F. Gantt. 1972. Perinatal behavior of northern elephant seal females and their young. Behaviour, 43:121–156.

Le Boeuf, B. J., D. P. Costa, A. C. Huntley, and S. D. Feldkamp. 1988. Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris.* Canadian Journal of Zoology, 66:446–458.

Le Boeuf, B. J., Y. Naito, A. C. Huntley, and T. Asaga. 1989*b*. Prolonged continuous, deep diving by northern elephant seals. Canadian Journal of Zoology, 67:2514–2519.

Le Boeuf, B. J., D. P. Costa, A. C. Huntley, G. L. Kooyman, and R. W. Davis. 1986. Pattern and depth of dives in northern elephant seals, *Mirounga angustirostris.* Journal of Zoology (London), 208:1–7.

Lehman, N., R. K. Wayne, and B. S. Stewart. In press. Comparative levels of genetic variability in harbor seals and northern elephant seals as determined by genetic fingerprinting. *In* Recent advances in marine mammal science (I. L. Boyd, ed.). London Zoological Society Symposium 66.

Lenfant, C. 1969. Physiological properties of blood of marine mammals. Pp. 95–116, *in* The biology of marine mammals (H. T. Anderson, ed.). Academic Press, New York, 511 pp.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Ed. 10. Laurentii Salvii, Holmiae, 1:1–824.

Lyon, G. M. 1937. Pinnipeds and a sea otter from the Point Mugu shell mound of California. Publications of the University of California in Biological Sciences, 18:133–168.

Mate, B. R. 1969. Northern extension of range of shore occupation by *Mirounga angustirostris.* Journal of Mammalogy, 50:639.

———. 1970. Oldest tagged northern elephant seal recovered in Oregon. California Fish and Game, 56:137.

McGinnis, S. M. 1975. Peripheral heat exchange in phocids. Rapports et Procès-verbaux des Réunions Conseil International Pour L'exploration de la Mer, 169:481–486.

McGinnis, S. M., and T. P. Southworth. 1967. Body temperature fluctuations in the northern elephant seal. Journal of Mammalogy, 48:484–485.

———. 1971. Thermoregulation in the northern elephant seal, *Mirounga angustirostris.* Comparative Biochemistry and Physiology, 40:893–898.

McLaren, I. A. 1975. A speculative overview of phocid evolution. Rapports et Procès-verbaux des Réunions Conseil International Pour L'exploration de la Mer, 169:43–48.

Morejohn, G. V., and D. M. Baltz. 1970. Contents of the stomach of an elephant seal. Journal of Mammalogy, 51:173–174.

Morejohn, G. V., and K. T. Briggs. 1973. Post-mortem studies of northern elephant seal pups. Journal of Zoology (London), 171:67–77.

Odell, D. K. 1974. Seasonal occurrence of the northern elephant seal, *Mirounga angustirostris,* on San Nicolas Island, California. Journal of Mammalogy, 51:81–95.

———. 1977. Structure of northern elephant seal population breeding on San Nicolas Island, California, in 1971. Animal Behavior, 25:208–214.

Ortiz, C. L., D. P. Costa, and B. J. Le Boeuf. 1978. Water and energy flux in fasting weaned elephant seal pups, *Mirounga angustirostris.* Physiology Zoology, 51:166–178.

Ortiz, C. L., B. J. Le Boeuf, and D. P. Costa. 1984. Milk intake of elephant seal pups: an index of parental investment. The American Naturalist, 124:416–422.

Pernia, S. D., D. P. Costa, and C. L. Ortiz. 1989. Glomerular filtration rate in weaned elephant seal pups during natural, long term fasts. Canadian Journal of Zoology, 67:1752–1756.

Pernia, S., A. Hill, and C. L. Ortiz. 1980. Urea turnover during prolonged fasting in the northern elephant seal. Comparative Biochemistry and Physiology, 65B:731–734.

Peters, W. 1875. Uber eine neue Art von Seebaren, *Arctophoca gazella,* von den Kerguelen-Inseln. Monatsber. Konig. Preuss. Akad. Wiss. Berlin, 1875:393–399.

Petrinovich, L. F. 1974. Individual recognition of pup vocalization by northern elephant seal mothers. Zeitschrift fur Tierpsychologie, 34:308–312.

Pike, G. C., and I. B. MacAskie. 1969. Marine mammals of British Columbia. Bulletin of the Fisheries Research Board of Canada, 71:1–54.

Radford, K. W., R. T. Orr, and C. L. Hubbs. 1965. Reestablishment of the northern elephant seal (*Mirounga angustirostris*) off Central California. Proceedings of the California Academy of Sciences, 31:601–612.

Rasa, O. A. E. 1971. Social interaction and object manipulation in weaned pups of the northern elephant seal, *Mirounga angustirostris.* Zeitschrift fur Tierpsychologie, 29:82–102.

Ray, C. E. 1976. Geography of phocid evolution. Systematic Zoology, 25:391–406.

Rea, L. D., and D. P. Costa. 1992. Changes in standard metabolism during long-term fasting in northern elephant seal pups (*Mirounga angustirostris*). Physiological Zoology, 65: 97–111.

Reiter, J., K. J. Panken, and B. J. Le Boeuf. 1981. Female competition and reproductive success in northern elephant seals. Animal Behavior, 29:670–687.

Reiter, J., N. L. Stinson, and B. J. Le Boeuf. 1978. Northern elephant seal development: the transition from weaning to nutritional independence. Behavioral Ecology and Sociobiology, 3:337–367.

Repenning, C. A., C. E. Ray, and D. Grigorescu. 1979. Pinniped Biogeography. Pp.. 357–369, *in* Historical biogeography, plate tectonics, and the changing environment (J. Gray and A. Boucot, eds.). Oregon State University Press, Corvallis. 565 pp.

Rett, E. Z. 1952. The northern elephant seal on San Miguel Island, California. Journal of Mammalogy, 33:109.

Ribic, C. A. 1988. Maternal aggression in northern elephant seals: the effect of the pup. Canadian Journal of Zoology, 66:1693–1698.

Rice, D. W. 1968. Stomach contents and feeding behavior of killer whales in the eastern North Pacific. Norsk Hvalfangst-Tidende, 57:35–38.

Riedman, M., and B. J. Le Boeuf. 1982. Mother-pup separation and adoption in northern elephant seals. Behavioral Ecology and Sociobiology, 11:203–215.

Riedman, M., and C. L. Ortiz. 1979. Changes in milk composition during lactation in the northern elephant seal. Physiological Zoology, 52:240–249.

Roletto, J., and R. Van Syoc. 1986. The occurrence of *Lepas anatifera* on *Zalophus californianus* and *Mirounga angustirostris.* California Fish and Game, 72:124–126.

Rothschild, W. 1910. Notes on sea elephants. Novitates Zoologicae, 17:445–446.

Rowly, J. 1921. Elephant seals off the coast of California. Journal of Mammalogy, 2:235–236.

Sandegren, F. E. 1976. Agonistic behavior in the male northern elephant seal. Behaviour, 57:136–158.

Saunders, A. M., and R. C. Hubbard. 1966. Obstructive emphysema in an elephant seal, *Mirounga angustirostris.* Laboratory Animal Care, 16:217–223.

Scammon, C. M. 1869. Pinnipedia—The sea elephant. Proceedings of the Academy of Natural Sciences, Philadelphia, 1869: 61–63.

———. 1874. The marine mammals of the northwestern coast of North America. John Carmany and Company, San Francisco, 319 pp.

Scheffer, V. B., and K. W. Kenyon. 1963. Elephant seal in Puget Sound, Washington. Murrelet, 44:23–24.

Shipley, C., and G. Strecker. 1986. Day and night patterns of vocal activity of northern elephant seal bulls. Journal of Mammalogy, 67:775–778.

Shipley, C., M. Hines, and J. S. Buchwald. 1981. Individual differences in threat calls of northern elephant seal bulls. Animal Behavior, 29:12–19.

———. 1986. Vocalizations of northern elephant seal bulls: development of adult call characteristics during puberty. Journal of Mammalogy, 67:526–536.

Shipley, C., B. S. Stewart, and J. Bass. In press. Seismic communication in northern elephant seals. *In* Sensory abilities of aquatic mammals (J. Thomas, R. Kastelein, and A. Supin, eds.). Plenum Press, New York.

SHIPLEY, C., J. BUCHWALD, R. FISHER, AND J. STRECKER. 1983. Preliminary report on studies of northern elephant seals: nocturnal behavior and neuroanatomy. Pp. 170–177, *in* Proceedings of the Mugu Lagoon/San Nicolas Island Ecological Research Symposium (R. Dow, ed.). United States Navy, Point Mugu, California. 273 pp.

SIMPSON, J. G., W. G. GILMARTIN, AND S. H. RIDGWAY. 1970. Blood volume and other hematologic values in young elephant seals (*Mirounga angustirostris*). American Journal of Veterinary Research, 31:1449–1452.

STEIN, B. R. 1989. Bone density and adaptation in semiaquatic mammals. Journal of Mammalogy, 70:467–476.

STEWART, B. S. 1989. The ecology and population ecology of the northern elephant seal, *Mirounga angustirostris* Gill, on the Southern California Channel Islands. Ph.D. dissert., The University of California, Los Angeles, 198 pp.

———. 1992. Population recovery of northern elephant seals on the Southern California Channel Islands. Pp. 1075–1086, *in* Wildlife 2001: populations. (D. R. McCullough and R. H. Barrett, eds.). Elsevier Publishers, Ltd., London, 1163 pp.

STEWART, B. S., AND R. L. DELONG. 1990. Sexual differences in migrations and foraging behavior of northern elephant seals. American Zoologist, 30:44A.

———. In press *a*. Spatial and temporal distribution of foraging northern elephant seals. *In* Elephant seals. (B. J. Le Boeuf and R. M. Laws, eds.). University of California Press, Berkeley.

———. In press *b*. Seasonal dispersion and habitat use of foraging northern elephant seals. *In* Recent advances in marine mammal science (I. L. Boyd, ed.). London Zoological Society Symposium, 66.

STEWART, B. S., AND P. K. YOCHEM. 1984. Seasonal abundance of pinnipeds at San Nicolas Island, California, 1980–1982. Bulletin of the Southern California Academy of Sciences, 83: 121–132.

———. 1985. Radio-tagged harbor seal, *Phoca vitulina richardsi*, eaten by white shark, *Carcharodon carcharias*, in the Southern California Bight. California Fish and Game, 71: 113–115.

———. 1986. Northern elephant seals breeding at Santa Rosa Island, California. Journal of Mammalogy, 67:402–403.

———. 1987. Entanglement of pinnipeds in synthetic debris and fishing net and line fragments at the Southern California Channel Islands: 1978–1986. Marine Pollution Bulletin, 18: 336–339.

———. 1991. Northern elephant seals on the Southern California Channel Islands and El Niño. Pp. 234–243, *in* Pinnipeds and El Niño: responses to environmental stress. (F. Trillmich and K. A. Ono, eds.). Springer-Verlag, Berlin, 293 pp.

STEWART, B. S., P. K. YOCHEM, R. L. DELONG, AND G. A. ANTONELIS. In press *a*. Trends in abundance and status of pinnipeds on the Southern California Channel Islands. *In* Proceedings of the Third California Islands Symposium (F. G. Hochberg, ed.). Santa Barbara Botanic Gardens.

STEWART, B. S., ET AL. In press *b*. History and present status of the northern elephant seal population. *In* Elephant seals (B. J. Le Boeuf and R. M. Laws, eds.). University of California Press, Berkeley.

STROUD, R. K., AND M. D. DAILEY. 1978. Parasites and associated pathology observed in pinnipeds stranded along the Oregon coast. Journal of Wildlife Diseases, 14:292–296.

STROUD, R. K., AND T. J. ROFFE. 1979. Causes of death in marine mammals stranded along the Oregon coast. Journal of Wildlife Diseases, 15:91–97.

SULLIVAN, R. M. 1980. Seasonal occurrence and haulout use in pinnipeds along Humboldt County, California. Journal of Mammalogy, 61:754–759.

SWEENEY, J. C. 1974. Common diseases of pinnipeds. American Veterinary Medical Association, 165:805–810.

SYDEMAN, W. J., H. R. HUBER, S. D. EMSLIE, C. A. RIBIC, AND N. NUR. 1991. Age-specific weaning success of northern elephant seals in relation to previous breeding experience. Ecology, 72:2204–2217.

TOWNSEND, C. H. 1912. The northern elephant seal *Macrorhinus angustirostris* Gill. Zoologica, 1:159–173.

TSUYUKI, H. 1957. On the oils contained in various blubbers of northern elephant seal, *Mirounga angustirostris*. Scientific Reports of the Whales Research Institute of Tokyo, 12:235–240.

———. 1958. Component fatty acids of northern elephant seal, *Mirounga angustirostris*, oil. Scientific Reports of the Whales Research Institute of Tokyo, 13:323.

TSUYUKI, H., AND S. ITOH. 1966. Studies on the oils contained in blubber of a southern elephant seal. Scientific Reports of the Whales Research Institute of Tokyo, 20:213–220.

VAN CITTERS, R. L., O. A. SMITH, N. W. WATSON, AND D. L. FRANKLIN. 1965. Field study of diving responses in the northern elephant seal. Hvalradets Skrifter, 46:1.

VAN CITTERS, R. L., D. L. FRANKLIN, O. A. SMITH, N. W. WATSON, AND R. E. ELSNER. 1966. Cardiovascular adaptations to diving in the northern elephant seal *Mirounga angustirostris*. Comparative Biochemistry and Physiology, 16:267–276.

WALKER, L., AND S. CRAIG. 1979. Archaeological evidence concerning the prehistoric occurrence of sea mammals at Point Bennett, San Miguel Island. California Fish and Game, 65: 50–54.

WALLS, G. L. 1963. The vertebrate eye. Hafner Publishing Company, New York, 785 pp.

WHITE, F. N., AND D. K. ODELL. 1971. Thermoregulatory behavior of the northern elephant seal, *Mirounga angustirostris*. Journal of Mammalogy, 52:758–774.

WICKHAM, L. L., D. P. COSTA, AND R. ELSNER. 1990. Blood rheology of captive and free-ranging northern elephant seals and sea otters. Canadian Journal of Zoology, 68:375–380.

WILLETT, G. 1943. Elephant seal in southeastern Alaska. Journal of Mammalogy, 24:500.

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