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Abundance, Distribution, and Population Growth of the Northern Elephant Seal (*Mirounga angustirostris*) in the United States from 1991 to 2010

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Abstract

We report on the distribution and abundance of the northern elephant seal (*Mirounga angustirostris*) in the United States from 1991 to 2010. Pup production (i.e., births) was the principal metric used to characterize abundance, distribution, and population growth of the U.S. population and of each rookery in the U.S. Birth estimates were obtained from the literature and estimated from recent counts of adult females or counts of pups made during ground and aerial photographic surveys conducted during the pupping-breeding season at all rookeries in central California and the Channel Islands in southern California. A total of 40,684 pups were estimated to have been born at 11 rookeries in the U.S. in 2010. The two most productive rookeries as of 2010 were San Miguel Island (16,208 pups) and San Nicolas Island (10,882 pups). The Piedras Blancas rookery was not established in 1991 but has since grown to be the fourth largest rookery as of 2010. Rookeries grew most rapidly initially, presumably due to high immigration rates; then increased moderately, eventually becoming stable; and some declined in size. Since 1988, the U.S. population has been growing at an average annual rate of 3.8%. The multiplicative factor needed to estimate total population size from pup production is estimated at 4.4. Total U.S. population size in 2010 was estimated at 179,000 individuals. Using conservative estimates for population growth of northern elephant seals in Mexico, we estimate that the total population in Mexico and the U.S. in 2010 was between 210,000 and 239,000 individuals.

Key Words: population growth, marine mammal census, pinniped, northern elephant seal, *Mirounga angustirostris*

Introduction

The northern elephant seal (*Mirounga angustirostris*) was nearly driven to extinction during the 19th century by commercial sealers (Townsend, 1912; Bartholomew & Hubbs, 1960). A few northern elephant seals (estimated at fewer than 100) survived at Guadalupe Island, Mexico (Bartholomew & Hubbs, 1960; Hoelzel et al., 1993). Subsequent population growth and range expansion during the 20th century has been well-documented (see Stewart et al., 1994). In the early 21st century, northern elephant seals could be found at many island and mainland haulout sites in western Mexico and the United States (Figure 1). The present population shows little genetic diversity (Hoelzel et al., 1993) as a result of the genetic bottleneck due to the catastrophic population reduction in the 19th century (Bonnell & Selander, 1974).

As the northern elephant seal population grew, population expansion, distribution, and growth were observed at all rookeries in the U.S. and Mexico (Stewart et al., 1994). Stewart et al. (1994) estimated that 28,000 pups were born in Mexico and the U.S. in 1991 and that the total population (including northern elephant seals in Mexico and the U.S.) was 112,000 of which 75% resided in the U.S.

The annual number of births (i.e., pup production) is used to depict population distribution and to estimate population growth and abundance

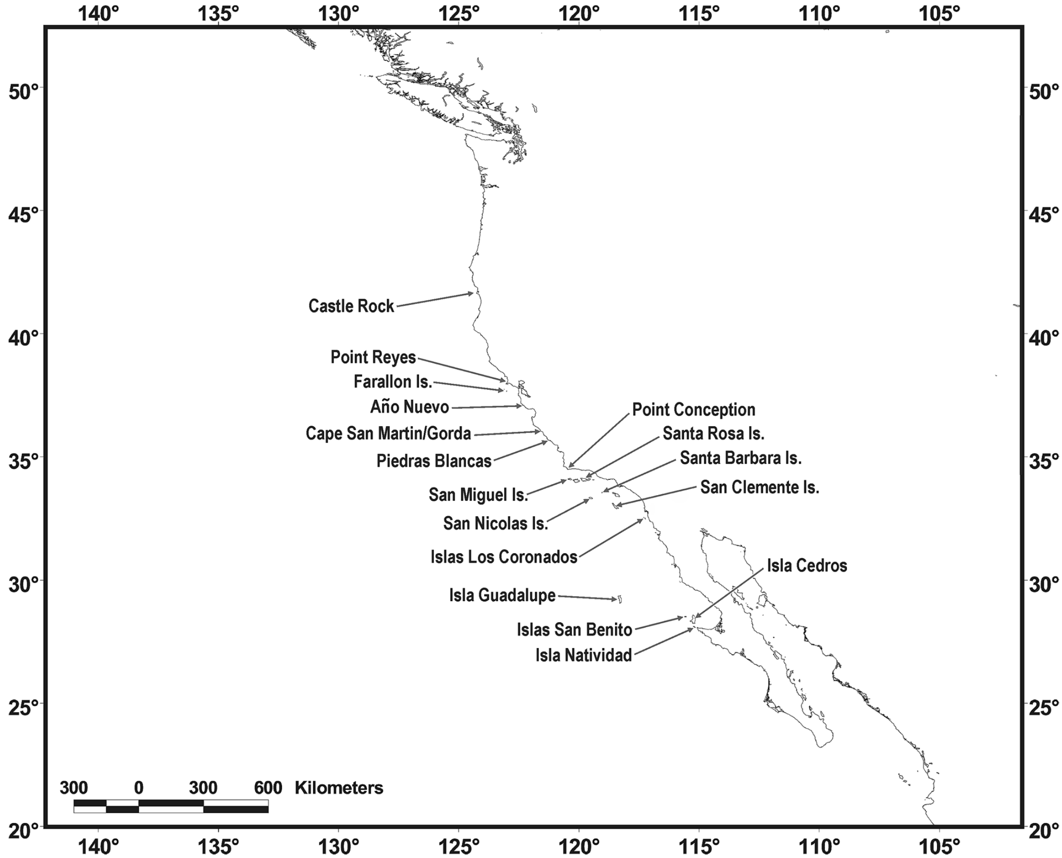

Figure 1. Northern elephant seal (*Mirounga angustirostris*) rookeries in the U.S. and Mexico

because not all age/sex classes are present on land at the same time. Northern elephant seal births have been estimated from counts made by biologists on the ground (Stewart et al., 1994) and from aerial photographs (Lowry, 2002). Aerial photographic counts of northern elephant seals used in this report were found to be precise and accurate (Lowry et al., 1996). Herein, we (1) provide new or revised birth estimates for northern elephant seals at all U.S. rookeries through 2010 and include previously published estimates from Stewart et al. (1994), (2) estimate population growth at each U.S. rookery and for the U.S. population, (3) derive a new factor for converting birth estimates to population abundance, and (4) provide a population estimate for northern elephant seals in the U.S. in 2010.

Methods

Censuses

Censuses of northern elephant seal rookeries at the Channel Islands in southern California and central California from Point Conception to Point Reyes, where almost the entire U.S. population resides, were made by biologists on the ground and from aerial photographic surveys conducted during the winter pupping-breeding season (December to March). A minimum of one census of live pups was made each year near the end of the breeding season; counts of dead pups were included in most of these censuses. At some locations, additional censuses were conducted earlier in the breeding season to document the total number of adult females.

Ground Surveys

Ground surveys were made by one or more biologists over several days, depending on the size of the island or rookery. Northern elephant seals were tallied (with the aid of mechanical hand-counters when necessary) while being observed by eye or through a hand-held binocular (refer to Stewart et al., 1994, for more details).

Aerial Photographic Surveys

Aerial photographic surveys were conducted with a twin-engine, high-winged Partenavia PN68 or

Partenavia PN68-Observer model aircraft flown at a ground speed of 185 km/h and at an altitude between 213 and 243 m. Multiple overlapping photographic passes were made over coastlines and beaches to ensure that all northern elephant seals on land were photographed (Lowry et al., 1996).

From 1988 to 2005, census photographs were taken with a 126-mm format Chicago Aerial Industries, Inc. KA-45A or KA-76 camera equipped with forward motion compensation and operated at a cycle rate that achieved 67% overlap between adjacent frames. In 2010, the northern elephant seals were photographed with a Canon EOS-1Ds Mark III, 20 megapixel digital camera attached to a mount having forward motion compensation and operated at a cycle rate that achieved 40% overlap between adjacent frames. The geographical position of each photograph was recorded by linking the camera (mounted vertically inside the belly of the aircraft) to a computer and Global Positioning System (GPS) receiver. A 152-mm-focal-length lens was used with the 126-mm format camera, and a 50- or 85-mm-focal-length lens was used with the Canon EOS-1Ds Mark III digital camera. Each camera was set at an aperture of f/5.6 with a shutter speed between 1/400 and 1/5,000 s. Three types of film were used in the 126-mm format camera: (1) Kodak Aerochrome MS Film 2448, a very fine-grained, medium-speed, color transparency film, was used during 1987-1999; (2) Aerochrome HS Film SO-359, a very fine-grained, high-speed, color transparency film, was used from 1997 to 2005; and (3) KODAK Aerochrome III MS Film 2427, a very fine-grained, medium-speed, color-reversal aerial film was used in 2005.

With color film, northern elephant seals were counted through a 7-70X zoom binocular microscope as the transparencies were illuminated on a light table. Images of animals were counted and marked on a clear acetate sheet with a different colored pen for each age/sex class category. Marks on the acetate were compared and verified with overlapping photographs. With digital photographs, animals were counted on computer monitors using Adobe *Photoshop CS5 Extended* software. Prior to counting the northern elephant seals, mosaics of coastline segments were created from multiple digital images using Adobe *Photoshop CS5* because digital photographs were too small and covered too small an area. As the animals were counted, they were recorded in one of the following age/sex class categories: (1) live pups, (2) dead pups, (3) juveniles, (4) adult females, and (5) subadult and adult males.

Estimate of Births

Births were estimated for all northern elephant seal rookeries in southern and central California during the winter pupping-breeding season. Births were estimated from counts of live and dead pups and by either of two methods from an estimate of the number of adult females present at the rookery during the entire pupping-breeding season. Le Boeuf & Reiter (1988) determined that 97.5% of adult females present at the rookery during the entire breeding season gave birth to a pup. Therefore, the number of births can be estimated as 97.5% of adult females during the entire breeding season. However, not all adult females are present at the same time during the pupping-breeding seasons (i.e., adult females are an asynchronous population) and were found to be present for approximately 32 or 33 d during the 2½ to 3 mo breeding season (Le Boeuf & Laws, 1994). Two methods have been devised for estimating the total number of adult females at the rookery: (1) total number of adult females was assumed to be the count of adult females at peak time (usually a specifically determined date at the end of January) plus the count of adult females 32 or 33 d prior and after that date; and (2) the total numbers of adult females was estimated with an equation that calculates the total number of adult females in an asynchronous population from three or more censuses of adult females during the breeding season (Condit et al., 2007). At this time, it is unknown which method is best. Ground counts of adult females can easily be done using the 32 or 33 d method, but it may require more than one person to census a large rookery in a single day. Aerial photographic surveys can census several large rookeries in a single day but are difficult or impossible to carry out at 32 or 33 d intervals due to weather and aircraft availability. These two methods or direct counts of pups, or a combination of them, were used by the authors to estimate total number of births:

1. Direct count of live pups at the end of the breeding season was used at Piedras Blancas rookery in 1992 and 1993.
2. Direct count of live and dead pups at or near the end of the breeding season was used at rookeries located at Santa Barbara Island (1983-2010), Piedras Blancas (1994-2001), Cape San Martin/Gorda (1992-2010), Point Reyes (1981-1991), and at Año Nuevo (1961-1967).
3. Taking 97.5% of the estimate of total number of adult females counted during three censuses 32 or 33 d apart was used at Point Reyes (1993-2010) and Piedras Blancas (2002-2010).
4. Taking 97.5% of the estimate of total number of adult females using an equation that estimates total number of adult females in an asynchronous population from three or more counts of adult females was used at the Año Nuevo rookery during 1968 to 2010 (Le Boeuf et al., 2011) and at San Nicolas Island rookery in 2010.

5. Dead pups counted on aerial photographs taken during the mid to late February aerial census had a correction factor applied to them to compensate for dead pups washed off the beach or buried. The correction factor was based on six counts of adult females at San Nicolas Island in 2010 that was used in the equation that estimated total number of adult females and, subsequently, live births. The total number of live pups counted from the mid to late February 2010 aerial photo census was subtracted from that value to estimate total pup mortality. Dead pups counted from the 2010 mid to late February aerial census were then estimated to represent 26.6% of total pup mortality, the inverse of which yielded a multiplier (3.76) that converts the number of dead pups counted from aerial photographs to total pup mortality. The 3.76 multiplier was then applied to the count of all dead pups from all aerial photographic censuses taken at all Channel Islands colonies during mid to late February 1988 to 2010 censuses to estimate total pup mortality, which was then added to the total number of live pups counted in the mid to late February aerial censuses to estimate births.
6. The rookery at Santa Barbara Island experiences high pup mortality rate due to narrow beaches that are susceptible to high tides and large waves. For aerial photo surveys of this rookery, either the maximum count of pups or 97.5% of adult females counted from a mid to late February aerial census was used to estimate births.
7. The rookery at San Clemente Island is very small and is censused during the last week in January. Births were estimated from the count of live plus dead pups, or from 97.5% of adult females, whichever was greater.

Population Growth and Trends

Northern elephant seal birth estimates were used to estimate U.S. population growth rate and the growth rate of each rookery in central and southern California. The annual rate of increase (λ) is calculated by the equation $\lambda = e^r$, where r is the slope of the linear regression from a series of natural log-transformed (ln) counts (Eberhardt & Simmons, 1992) obtained at the same time each year.

A posteriori examination of northern elephant seal birth estimates indicated non-linear growth of birth estimates over time for individual northern elephant seal rookeries and for regional summations of birth estimates (e.g., central California, Channel Islands, and U.S. populations). While some rookeries showed an increase in births, others showed an increase followed by a decrease in later years, or a slowing of the growth rate as time progressed. Breakpoint linear regression analysis (also known as piecewise regression analysis) of natural log-transformed birth estimates identified breakpoints in time series data. The program *SegReg* (www.waterlog.info/segreg.htm) was used to determine the location of the breakpoints in the time series of birth estimates and to perform linear regression analysis ($y = a + bx$) on each segment time-interval from which the growth rate could be calculated for each segment. In some cases, no breakpoints were detected in the time interval. For each time-interval segment, the following was tabulated: (1) the average annual rate of increase (λ) calculated from the slope of the regression, (2) number of observations (y) having birth estimates used in the analysis, (3) coefficient of determination (R^2), and (4) coefficient of variation (CV) of the average annual growth rate (slope of the regression divided by the standard error of the slope).

Total Population Size from Birth Estimates

A multiplicative factor for estimating the total population size from birth estimates was estimated by constructing a large number of life tables based on published ranges of survival and fecundity rates of elephant seals. For any complete life table (fecundity plus gender-specific survival at every age), there is a corresponding stable population growth rate, λ, defined as N_t/N_{t-1} (population sizes in consecutive years) and stable age distribution, defined as n_x/N_t, where n_x is the population size at age x at any time, and N is the total population at the same time. To find λ and the age distribution of both sexes, we simulated n_x in a population subject to a specified life table until they stabilized. The pup multiplier was then found as $M = N/n_o$, where n_o is the number of pups born. Moreover, assuming half of all births are male, the sex ratio at every age also stabilizes, and a multiplier for both males and females can be found. Our goal was to replicate a large number of life tables, covering published ranges of survival and fecundity, in order to estimate M, its variance, and how it relates to λ.

To generate many life tables, demographic rates were collected from published studies on annual survival and fecundity in northern and southern (*Mirounga leonina*) elephant seals (Cooper & Stewart, 1983; Le Boeuf & Reiter, 1988; Hindell, 1991; Huber et al., 1991; Reiter & Le Boeuf, 1991; Clinton & Le Boeuf, 1993; Le Boeuf et al., 1994; Pistorius & Bester, 2002; McMahon et al., 2003; Pistorius et al., 2004; Condit et al., 2013). From each study, if annual rates were included from > 1 y, we averaged across years, but different colonies were kept separate. Survival rates were averaged separately in four juvenile ages and two broad age categories in adults (Table 1). Fecundity, defined as pups weaned per female (thus including pregnancy less pup mortality), was averaged in two age categories (Table 1). The highest and lowest rates found across all studies are shown in Table 1. These ranges were converted to logit-normal distributions that produced the matching

95% confidence interval—that is, we found the mean and standard deviation (SD) of a logit-normal distribution that would produce rates falling in each desired range (Table 1). Life tables were then constructed stochastically using random draws from these logit-normal distributions, assuming no correlation among any of the rates. We created 100,000 life tables and simulated each to find its corresponding λ and M. The results were assembled into seven bins based on population growth, and in each λ bin, the mean and SD of M were calculated. We report the mean ± 1.96 SD.

Results

In 2010, 40,684 northern elephant seal pups are estimated to have been born in the U.S. (Table 2). Since 1988, the U.S. population has been growing (Figure 2) at an average annual rate of 3.8% (λ = 1,038; Table 3). The largest northern elephant seal rookery in 2010 was located at San Miguel Island (16,208 births), followed by San Nicolas Island (10,882 births), Santa Rosa Island (5,946 births), and Piedras Blancas (4,469 births) (Table 2). Of these four rookeries, in 2010, the Santa Rosa Island

Table 1. Annual survival and fecundity rates gleaned from the literature on northern and southern elephant seals (*Mirounga angustirostris* and *M. leonina*); the logit mean and SD describe a Gaussian distribution of logit-transformed rates which match the range of rates taken from the literature.

Age (y)	Sex	Rate	Range	Logit mean ± SD
1	Both	Survival	0.33-0.78	0.279 ± 0.493
2	Both	Survival	0.67-0.91	1.511 ± 0.401
3	Both	Survival	0.74-0.82	1.281 ± 0.118
4	Both	Survival	0.68-0.87	1.327 ± 0.287
5-16	Female	Survival	0.78-0.89	1.678 ± 0.206
17-21	Female	Survival	0.56-0.73	0.618 ± 0.188
5-10	Male	Survival	0.67-0.74	0.877 ± 0.084
10-15	Male	Survival	0.57-0.67	0.495 ± 0.107
3	Female	Fecundity	0.13-0.36	-1.238 ± 0.331
≥ 4	Female	Fecundity	0.72-0.94	1.848 ± 0.452

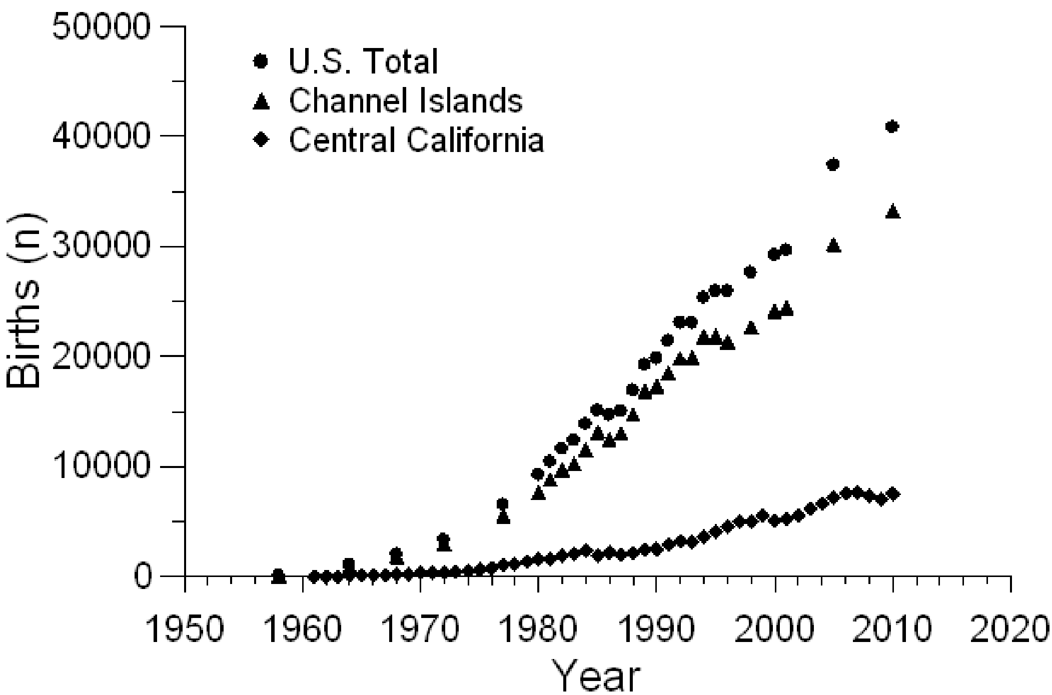

Figure 2. Total number of northern elephant seal births at the Channel Islands in southern California, along the coast in central California, and in the U.S. as a whole

Table 2. Birth estimates of northern elephant seals for rookeries in the United States

	Central California							Channel Islands						
Year	Point Reyes	South Farallon Islands	Año Nuevo Island and mainland	Cape San Martin/ Gorda	Piedras Blancas	Point Conception	Total	San Miguel Island	Santa Rosa Island	San Nicolas Island	Santa Barbara Island	San Clemente Island	Total	U.S. total
1958							0	84[a]					84	132[l]
1959										48[a]				
1960														
1961			12[g]				12							
1962			23[g]				23							
1963			32[g]				32							
1964			60[g]				60	878[a]		83[a]	11[a]		972	1,032
1965			75[g]				75							
1966			100[g]				100			136[a]				
1967			143[g]				143							
1968			187[g]				187	1,624[a]		171[a]			1,823	2,010
1969			238[g]				238			193[a]				
1970			307[g]				307			210[a]				
1971			326[g]				326			354[a]				
1972		1[a]	390[g]				391	2,482[a]		428[a]	28[a]	0[a]	2,938	3,329
1973		2[a]	435[g]				437	3,088[a]						
1974		17[a]	495[g]				512							
1975		35[a]	622[g]				657	3,547[a]						
1976		60[a]	755[g]				815	4,014[a]						
1977		104[a]	891[g]				995	4,760[a]		693[a]	74[a]	1[a]	5,528	6,523
1978		133[a]	998[g]				1,131	5,447[a]						
1979		184[a]	1,146[g]				1,330	5,531[a]	0					
1980		232[a]	1,368[g]				1,600	6,475[a]	0[a]	1,187[w]			7,662	9,262
1981	1[a]	292[a]	1,313[g]	3[a]			1,609	7,272[a]	0[a]	1,546[w]			8,818	10,427
1982	1[a]	367[a]	1,511[g]	18[a]			1,897	7,376[a]	0[a]	2,312[w]		4[k]	9,692	11,589
1983	2[a]	475[a]	1,639[g]	7[a]			2,123	8,301[a]	0[a]	1,906[a]	25[k]	0[k]	10,232	12,355
1984	12[a]	447[a]	1,854[g]	25[a]			2,338	9,342[a]	0[a]	2,074[a]	80[k]	3[k]	11,499	13,837
1985	15[a]	360[a]	1,541[g]	24[a]			1,940	10,459[a]	2[a]	2,583[a]	93[k]	2[k]	13,139	15,079

Year	Central California							Channel Islands						
	Point Reyes	South Farallon Islands	Año Nuevo Island and mainland	Cape San Martin/ Gorda	Piedras Blancas	Point Conception	Total	San Miguel Island	Santa Rosa Island	San Nicolas Island	Santa Barbara Island	San Clemente Island	Total	U.S. total
1986	19[a]	434[a]	1,726[g]	4[a]			2,183	9,824[a]	0[a]	2,626[a]	56[k]	1[k]	12,507	14,690
1987	20[a]	395[a]	1,548[g]	13[a]			1,976	10,120[a]	2[a]	2,835[a]	75[k]	1[k]	13,033	15,009
1988	34[a]	393[a]	1,738[g]	13[a]			2,178	11,405[k]	2[a]	3,248[k]	69[k]	0[k]	14,724	16,902
1989	44[a]	380[a]	1,905[g]	67[a]			2,396	11,799[k]	3[a]	4,925[k]	106[k]	0[k]	16,833	19,229
1990	52[a]	396[a]	2,004[g]	65[a]			2,517	12,929[k]	27[a]	4,266[k]	69[k]	0[k]	17,287	19,804
1991	81[a]	352[a]	2,200[g]	263[a]			2,896	13,638[k]	86[k]	4,739[k]	45[k]	3[k]	18,511	21,407
1992	116[b]	370[f]	2,366[g]	371[h]	1[i]		3,224	13,970[k]	67[k]	5,775[k]	18[k]	3[k]	19,833	23,057
1993	149[b]	329[f]	2,168[g]	416[h]	54[i]		3,116	14,397[k]	123[k]	5,310[k]	106[k]	2[k]	19,938	23,054
1994	228[b]	287[f]	2,276[g]	471[i]	293[i]		3,555	15,451[k]	315[k]	5,964[k]	47[k]	0[k]	21,777	25,332
1995	150[b]	299[f]	2,731[g]	277[i]	605[i]		4,062	14,704[k]	186[k]	6,821[k]	110[k]	12[k]	21,833	25,895
1996	290[b]	312[f]	2,484[g]	511[i]	989[i]		4,586	14,421[k]	435[k]	6,353[k]	112[k]	16[k]	21,337	25,923
1997	356[b]	274[f]	2,720[g]	506[i]	1,196[i]		5,052					18[k]		
1998	381[b]	250[f]	2,554[g]	122[i]	1,671[i]		4,978	15,236[k]	516[k]	6,828[k]	34[k]	17[k]	22,631	27,609
1999	408[c]	198[f]	2,575[g]	431[i]	1,912[i]		5,524					13[k]		
2000	376[c]	174[f]	2,416[g]	224[i]	1,846[i]		5,036	12,541[k]	1,527[k]	10,018[k]	67[k]	7[k]	24,160	29,196
2001	402[c]	156[f]	2,473[g]	266[i]	1,941[i]		5,238	13,365[k]	1,575[k]	9,403[k]	50[k]	17[k]	24,410	29,648
2002	427[c]	136[f]	2,466[g]	362[i]	2,176[i]		5,567					20[j]		
2003	495[c]	149[f]	2,594[g]	305[i]	2,649[i]		6,192					19[j]		
2004	642[c]	156[f]	2,512[g]	299[i]	3,053[i]		6,662					24[j]		
2005	643[c]	158[f]	2,619[g]	231[i]	3,514[i]	6[j]	7,171	15,634[j]	4,227[j]	10,245[j]	55[j]	46[j]	30,207	37,378
2006	746[d]	185[f]	2,582[g]	278[i]	3,789[i]		7,580					29[j]		
2007	705[e]	168[f]	2,470[g]	250[i]	4,080[i]		7,673					46[j]		
2008	683[e]	150[f]	2,368[g]	184[i]	4,007[i]		7,392					63[j]		
2009	680[e]	124[f]	2,199[g]	204[i]	3,808[i]		7,015					57[j]		
2010	698[c]	120[f]	2,144[g]	101[i]	4,469[i]	8[j]	7,540	16,208[j]	5,946[j]	10,882[j]	51[j]	57[j]	33,144	40,684

[a] From Stewart et al. (1994); [b]Sydeman & Allen (1999); [c]National Park Service, unpub. data; [d]Adams et al. (2007); [e]Allen et al. (2012); [f]Berger (2011); [g]Le Boeuf et al. (2011); [h]R. Jameson, unpub. data (provided by B. Hatfield); [i]B. Hatfield, unpub. data; [j]M. Lowry, unpub. data (*Births = live pups + 3.76*dead pups; or births = 0.975*adult females*); [k]Lowry (2002) (*Births = live pups + 3.76*dead pups; or births = 0.975*adult females*); and [l]the 1959 count from San Nicolas Island was added to the 1958 count at San Miguel because pups were likely being born at both islands, but both were not visited during the same year.

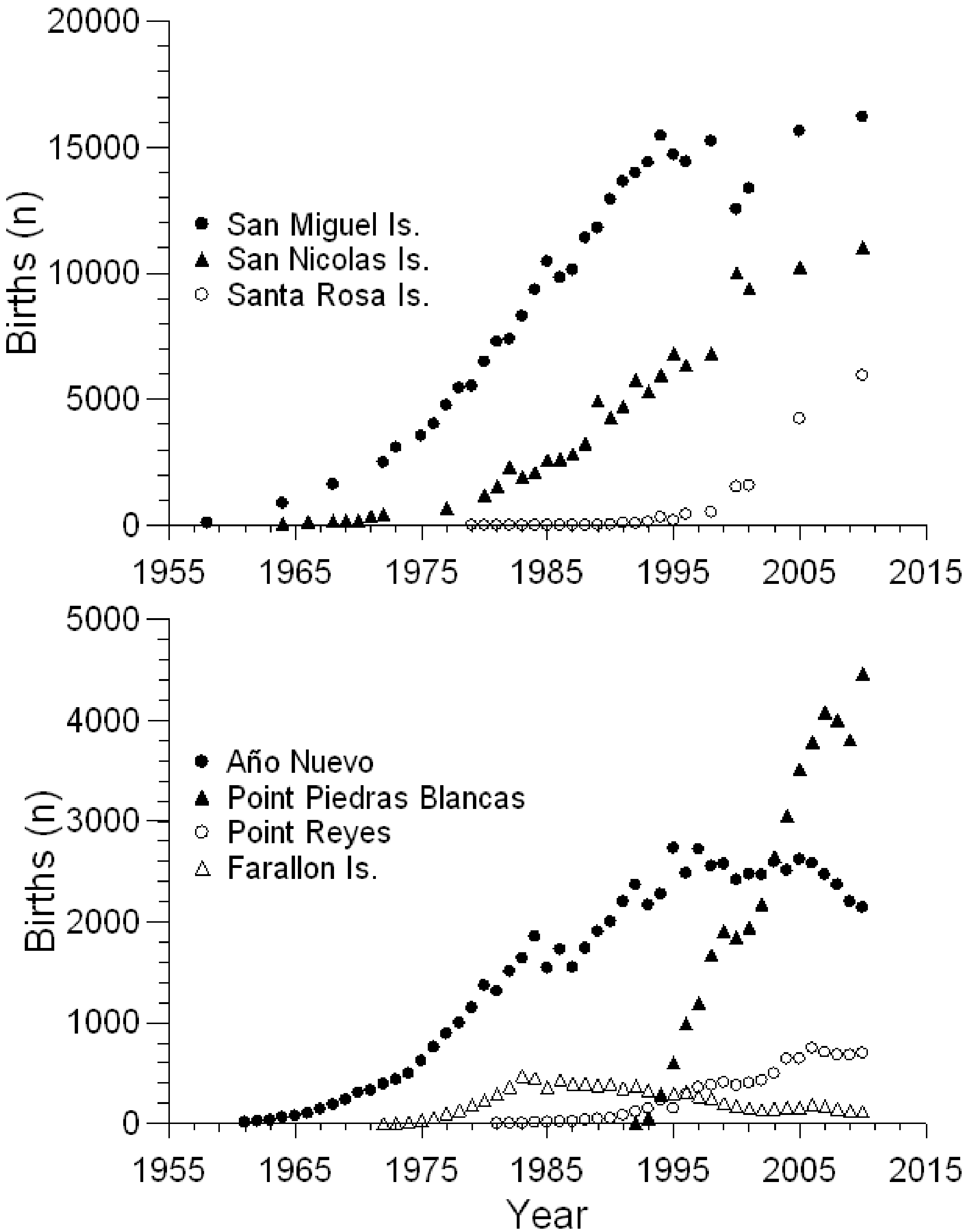

Figure 3. Northern elephant seal births at rookeries in the U.S.

rookery experienced the highest average annual growth rate (45.6%, λ = 1.456), followed by San Nicolas Island (11.9%, λ = 1.119) and Piedras Blancas (10.8%, λ = 1.108). The rookeries at San Miguel Island appear to be leveling off (λ = 1.005; Table 3). In 2010, the rookeries at the Farallon Islands, Año Nuevo, Cape San Martin/Gorda, and Santa Barbara Island were declining (Figure 3; Table 3).

The multiplicative factor, *M*, needed to estimate total population size from the number of births was 4.4 when population growth rate λ was > 1.02 (Table 4), with a 95% confidence interval spanning 3.8 to 5.0. *M* did not vary much with λ, averaging nearly 4.2

Table 3. Average annual rate of increase (λ), number of observations (n), coefficient of determination (R^2), and coefficient of variation (CV) for the rates of increase that were computed for year-intervals chosen by breakpoint regression analysis of log-transformed northern elephant seal birth estimates for rookeries in the U.S.

Rookery	Year interval	n	R^2	λ	CV
Point Reyes	1981-1992	12	0.91	1.541	0.098
	1993-2010	18	0.86	1.092	0.102
Farallon Islands	1973-1980	8	0.85	1.808	0.168
	1981-2010	30	0.84	0.955	-0.084
Año Nuevo	1961-1977	17	0.95	1.279	0.061
	1978-1995	18	0.89	1.048	0.088
	1996-2010	15	0.40	0.991	-0.337
Cape San Martin/Gorda	1981-1994	14	0.77	1.440	0.157
	1995-2010	16	0.29	0.951	-0.417
Piedras Blancas	1992-1995	4	0.89	8.090	0.251
	1996-2010	15	0.94	1.108	0.073
San Miguel Island	1958-1979	10	0.92	1.197	0.106
	1980-1990	11	0.95	1.067	0.076
	1991-2010	11	0.15	1.005	0.793
Santa Rosa Island	1985-2010	16	0.87	1.456	0.102
San Nicolas Island	1964-2010	27	0.92	1.119	0.059
Santa Barbara Island	1964-1983	5	0.30	1.051	0.872
	1983-2010	18	0.06	0.984	-1.015
San Clemente Island	1977-2010	24	0.87	1.155	0.081
Central California	1958-1970	11	0.93	1.547	0.092
	1971-1979	9	0.99	1.200	0.030
	1980-2010	31	0.96	1.059	0.036
Channel Islands	1958-1987	13	0.92	1.164	0.091
	1988-2010	14	0.95	1.034	0.065
United States	1958-1987	13	0.92	1.170	0.091
	1988-2010	14	0.96	1.038	0.058

Table 4. Estimated multipliers for deriving total population size from the number of northern elephant seal births (with 95% confidence limits [CL] in parentheses) as a function of population rate of increase (λ; i.e., population growth rate); the multiplier (M) for females gives the total female population size from female pups, and likewise for males; M for the total population is their mean.

	Female		Male		Total population	
λ	Multiplier	95% CL	Multiplier	95% CL	Multiplier	95% CL
0.95-0.96	4.70	(4.15-5.24)	3.62	(2.92-4.31)	4.16	(3.28-5.04)
0.97-0.98	4.77	(4.27-5.28)	3.71	(3.08-4.34)	4.24	(3.43-5.05)
0.99-1.00	4.83	(4.38-5.28)	3.78	(3.22-4.34)	4.31	(3.59-5.02)
1.01-1.02	4.88	(4.47-5.28)	3.84	(3.35-4.33)	4.36	(3.72-4.99)
1.02-1.03	4.89	(4.51-5.28)	3.86	(3.41-4.32)	4.38	(3.78-4.97)
1.03-1.04	4.91	(4.57-5.25)	3.88	(3.48-4.28)	4.39	(3.87-4.92)
≥ 1.04	4.91	(4.60-5.22)	3.88	(3.51-4.26)	4.40	(3.91-4.88)

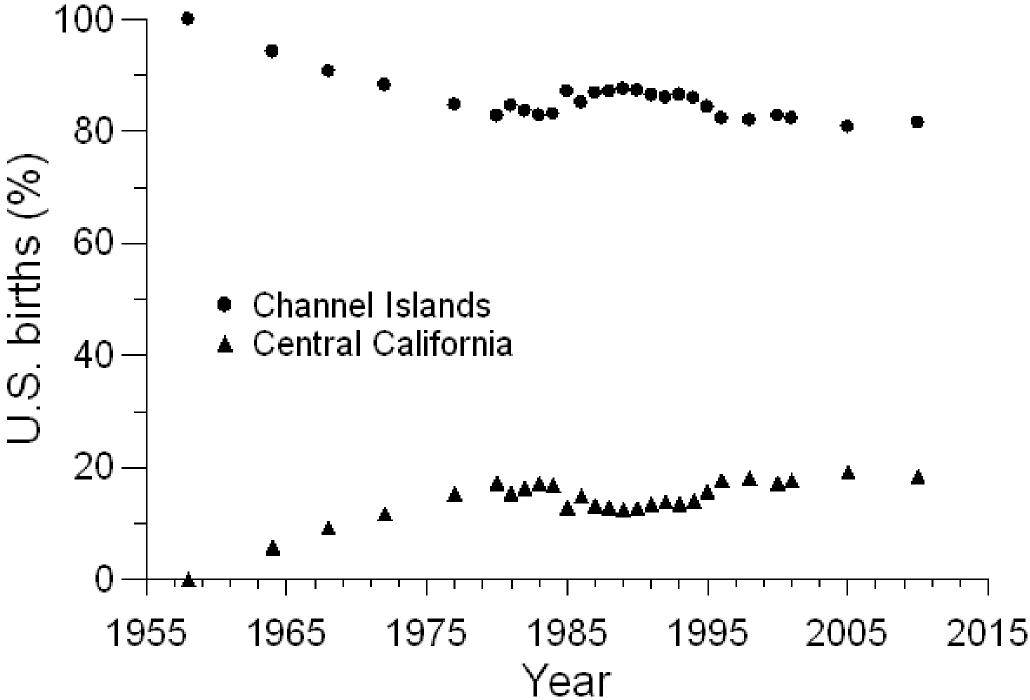

Figure 4. Percentage of U.S. northern elephant seal births recorded at rookeries at the Channel Islands in southern California and along the coast in central California

at the lowest rates of population growth and never higher than 4.4 (Table 4). Rather, most uncertainty in *M* was due to uncertainty in demographic rates (Table 1). With fecundity (including pre-weaning pup survival) as low as it has been observed (forcing survival to be its highest), *M* reached values near 5.0. Conversely, if fecundity were as high as it has been observed (so that survival must be low), then *M* fell < 4.0. The pup multiplier for males (male pups converted to total males) was lower than for females (Table 4) because of lower survival rates in adult males relative to females (Table 1).

Total U.S. northern elephant seal population size in 2010 is estimated at 179,000 (2.5% = 159,000, 97.5% = 199,000). Expansion of the U.S. population of northern elephant seals was due primarily to growth at Channel Islands rookeries in southern California (Figure 2). Channel Islands rookeries accounted for 81.5% of births in 2010, with the remaining 18.5% of births occurring in central California (Figure 4). Since 1988, northern elephant seal births at the Channel Islands have been increasing at an average annual growth rate of 3.4% ($\lambda = 1.034$, CV = 0.065), and at an average annual growth rate of 5.9% ($\lambda = 1.059$, CV = 0.036; Table 3) in central California since 1980.

Discussion

The U.S. population estimate for 2010 exceeds the last estimate made in 1991 by Stewart et al. (1994). Although we do not have current birth estimate data for the population of northern elephant seals in Mexico, if both populations experienced similar growth rates since the 1991 estimate, then the total northern elephant seal population in 2010 was roughly 239,000 individuals. However, Stewart et al. reported that the population in Mexico had stabilized in 1991. If the population in Mexico did not grow, then the total population estimate for the species in 2010 would be roughly 210,000 individuals. It would be reasonable to say, then, that in 2010 the combined northern elephant seal population in Mexico and the U.S. included 210,000 to 239,000 individuals.

The U.S. northern elephant seal population continues to grow, with most of the growth occurring at the larger rookeries in southern California. New rookeries show a period of extremely fast growth in the first few years, presumably due to immigration because the initial rate of growth is not biologically feasible, followed by a gradual slowing of the growth rate. Eventually, some rookeries, such as those at the Farallon Islands, Año Nuevo Point and Island, Cape San Martin/Gorda, and

Santa Barbara Island, experienced negative growth. As the Farallon Islands rookery diminished in size, the Point Reyes rookery increase probably resulted from northern elephant seals moving there from the Farallon Islands, Piedras Blancas, and Año Nuevo which are nearby (Condit et al., 2013). Growth at Piedras Blancas occurred as the Año Nuevo rookery began to decrease and as the San Miguel Island rookery decreased in 2000 and 2001. The Santa Rosa Island rookery increased due to immigration from San Miguel Island (which is next to it) as is shown by decreases in births at San Miguel Island in 2000 and 2001. Eventually, the number of births at San Miguel Island increased such that by 2005 and 2010, the number of births at that rookery exceeded the previous high level. When that happened, there were enough northern elephant seals at Santa Rosa Island to continue population expansion at that island. On occasion, a few pups have been produced at Castle Rock (Point Saint George) in northern California near Crescent City (Hodder et al., 1998). We did not count that site in 2010, but it generally has produced no more than 11 pups. Still further north, elephant seals have bred at Shell Island, Oregon, and Race Rocks and other sites in the Strait of Juan de Fuca, Washington, and British Columbia, but only a few pups are produced at these sites, and they rarely survive to weaning because of inclement weather (Hodder et al., 1998; Jeffries et al., 2000).

The pup multiplier we present is similar to those for earlier estimates for gray seals (*Halichoerus grypus*) and southern elephant seals, but no prior estimates have separated males and females or produced estimates of uncertainty. The uncertainty in M, caused mostly by uncertainty in demographic rates, adds about 20% uncertainty in total U.S. population size, thus our population estimate spans 159,000 to 199,000.

Northern elephant seal population expansion is expected to continue but at a reduced rate due to increased pup mortality at crowded rookeries. Sandy beaches (preferred terrestrial habitat) at San Nicolas Island and San Miguel Island are all almost totally occupied by elephant seals during the pupping-breeding season. The same will happen soon at Santa Rosa Island. Santa Cruz Island, Anacapa Island, and other Channel Islands either have a limited number of sandy beaches or none at all. The southern California coastline has suitable beaches, but human presence will probably keep northern elephant seals from occupying them. Point Reyes and Piedras Blancas rookeries have suitable and ample beach space for rookery growth nearby. The Point Conception rookery is extremely small as it lies in a small cove beneath a towering cliff and is occupied by Pacific harbor seals (*Phoca vitulina richardii*). There is, however, ample beach space available north of Point Arguello within Vandenberg Air Force Base that could possibly be occupied by northern elephant seals in the future.

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