Initial growth of northern fur seal (*Callorhinus ursinus*) colonies at the South Farallon, San Miguel, and Bogoslof Islands

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Understanding the colonization or recolonization of breeding sites used by colonial animals is fundamental to metapopulation theory and has practical applications in conservation biology. Historically, pinniped species were heavily exploited worldwide, resulting in some breeding colonies becoming extirpated. As populations recover, some abandoned sites may be recolonized or new sites can be colonized. We analyzed aerial and ground survey data on pup counts from 3 islands (South Farallon, San Miguel, and Bogoslof) (re)colonized by northern fur seals (*Callorhinus ursinus*), using classical and Bayesian state-space modeling approaches to describe population growth rates during their initial 21 years, with particular focus on the South Farallon Islands. We used information from tagged animals that immigrated to the South Farallon Islands from San Miguel Island to describe the age and sex structure of the founding recolonizers of the South Farallon Islands. We also examined the evidence for the generality of Roux's (1987) description of fur seal population recovery using a literature review of published fur seal population growth rates. We found the 3 colonies had different annual population growth rates (South Farallon = 34%, San Miguel = 45%, Bogoslof = 59%), but all were growing at rates among the fastest observed for fur seals worldwide. Immigrants from San Miguel to the South Farallon Islands were younger and female-biased relative to the tagged population at San Miguel Island. The general framework described by Roux (1987) was an effective description of observed fur seal population recovery. Our results inform our understanding of the initiation and growth of pinniped breeding colonies.

Key words: *Callorhinus ursinus*, colonization, fur seal, growth rate, immigration, metapopulation, population recovery

Understanding the process of (re)colonization (colonization or recolonization) of breeding sites used by colonial animals after extirpation is fundamental to metapopulation theory (Levins 1970; Hanski and Gilpin 1991), with applications in conservation biology and stock management (Gerber and Hilborn 2001; Lee et al. 2014). The topic of breeding colony initiation and growth has received some attention for seabirds (Oro and Ruxton 2001; Kildaw et al. 2005), but is less well developed for pinnipeds (Loughlin and Miller 1989). Pinniped species have been heavily exploited worldwide, resulting in the reduction of many populations during the 19th and 20th centuries (Bonner 1982). Some populations and subpopulations were so depleted that they were driven to near or total extinction (Gerber and

Hilborn 2001; Kovacs et al. 2012). During the course of these depletions, some breeding colonies became extirpated (Gentry 1998), but during population recovery (Lotze et al. 2011) abandoned sites were recolonized (Peterson et al. 1968; Pyle et al. 2001), or new sites colonized (Loughlin and Miller 1989).

The northern fur seal (*Callorhinus ursinus*) is a pelagic-feeding, polygynously breeding otariid, with an expansive range across the North Pacific Ocean and Bering Sea (Gentry 1998). The total northern fur seal population may have numbered 2–3 million when the first breeding island was discovered in 1742 (Gentry 1998), but during more than 2 centuries of commercial exploitation under various harvest regulations, the northern fur seal population fell and rose repeatedly (Roppel and Davey

1965; Gentry 1998). Commercial and experimental harvests ended in 1984, but the global population has been in overall long-term decline since the 1950s (York and Hartley 1981; Towell et al. 2006; Gelatt et al. 2015). The current world population of approximately 1.29 million animals now breed at 7 main sites. The largest of these are the Pribilof Islands, United States (St. Paul and St. George), which host approximately 45% of the global population, and the Commander Islands, Russia (Bering and Medny), which host ~20% of the population. Smaller rookeries exist on Tuleny (Robben) Island and the Kuril Islands in Russia as well as on Bogoslof Island, San Miguel Island, and the South Farallon Islands, United States (Gelatt et al. 2015). In addition to these historical changes, northern fur seals also had very different breeding and migration patterns in the pre-Columbian prehistoric period than during the historical period (Burton et al. 2001; Newsome et al. 2007).

Northern fur seals rarely colonize new sites, or recolonize abandoned breeding sites. Of 46 known breeding sites on North Pacific and Bering Sea islands, 18 were permanently extirpated since 1742 with only 2 recolonized, and 2 new sites formed (Gentry 1998). Likewise, abandoned or new islands are rarely (re)colonized. Northern fur seals were extirpated from the South Farallon Islands by sealers during the 1800s (Starks 1922; Townsend 1931; Scheffer and Kraus 1964), but fur seals recolonized, with the first observed birth of a pup in 1996 (Pyle et al. 2001). Bogoslof Island arose from volcanic activity in 1796 and was colonized by northern fur seals in 1980 (Lloyd et al. 1981). San Miguel Island was observed to be recolonized in 1968 (Peterson et al. 1968), after a 100- to 500-year period of absence of fur seals (Walker 1979; Erlandson et al. 2009). These (re)colonization events are few in relation to the hundreds of similar islands available for (re)colonization across the North Pacific and Bering Sea (Gentry 1998).

Population recovery is a continuous phenomenon, but Roux (1987) identified 4 phases in the recovery of fur seal populations defined by changes in population growth rate, spatial distribution, and density: 1) "survival" from the cessation of exploitation to the initiation of breeding; 2) "establishment," when breeding is restricted to a few founding colonies; 3) "recolonization," when numbers increase and new or renewed colonies arise rapidly; and 4) "maturity," indicated by a decline in the rate of increase due to density-dependent factors. Here, we focused on the recolonization phase by using aerial and ground survey data on pup counts analyzed using classical and Bayesian state-space modeling approaches to describe the population growth rate and spatial distribution of the colony of northern fur seals on the South Farallon Islands during its initial 21 years (from 1996 to 2016). We compared the South Farallon Islands with 2 other recently (re)colonized islands (San Miguel and Bogoslof) to determine whether and how population growth rates differed among sites. We used information from tagged animals that immigrated to the South Farallon Islands from San Miguel Island to describe the age and sex structure of the founding recolonizers. Finally, we examined the evidence for the generality of Roux's (1987) description of fur seal population recovery using a literature review of published fur seal population growth rates.

MATERIALS AND METHODS

Study sites.—Research was conducted at the South Farallon Islands (Fig. 1; 37°40′N, 123°00′W; 0.49 km²; comprised of Southeast Farallon Island and West End Island), 43 km west of San Francisco, California; San Miguel Island (34°02′N, 120°26′W; comprised of Adam's Cove and Castle Rock colonies), 60 km southwest of Santa Barbara, California; and Bogoslof Island (53°56′N, 158°02′W; 1.28 km²), 40 km north of Umnak Island in the eastern Aleutian Island chain.

The South Farallon and San Miguel islands are in the California Current ecosystem, where El Niño Southern Oscillation (ENSO) conditions produce large changes in the marine environment that result in the redistribution of and reduced prey availability for top marine predators that affect survival and reproduction (Sydeman and Allen 1999; Lee et al. 2007; Schmidt et al. 2014). The impact of ENSO events on the population growth of northern fur seals is an important regulatory mechanism in the California Current ecosystem (DeLong and Antonelis 1991; Orr et al. 2012).

In contrast to the South Farallons and San Miguel Island, Bogoslof Island is adjacent to the major pelagic feeding area used by northern fur seals within the Bering Sea (Zeppelin et al. 2015). Although far-reaching environmental factors such as ENSO may affect the climate of the Bering Sea on occasion (Overland et al. 2001), the climate of the southeastern Bering Sea is mostly influenced by the Pacific North American pattern and by the Arctic Oscillation (Overland et al. 1999). These patterns appear to have less impact on the productivity of the Bearing Sea ecosystem compared to ENSO impacts on the California Current ecosystem. Due to these differences in the
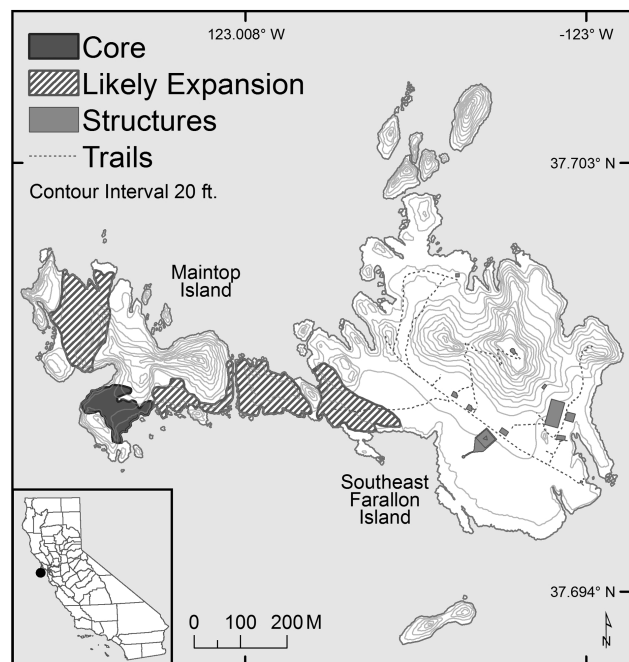

Fig. 1.—Map of the South Farallon Islands, California, showing the location of the northern fur seal (*Callorhinus ursinus*) breeding colony in 2016. Core breeding area, areas where we expect near-future expansion, and structures are marked.

local marine environments of the California Current and Bering Sea, we predicted that northern fur seal population growth rates of the South Farallons and San Miguel Island would be similar to each other and slower than at Bogoslof Island.

Research followed ASM guidelines (Sikes et al. 2016) and was conducted under National Marine Fisheries Service research permit #: 17152.

Ground-based surveys.—Biologists have conducted weekly counts of pinnipeds hauled out on the South Farallon Islands (Fig. 1) from an observation post at the lighthouse on the islands' highest point since 1970 (Sydeman and Allen 1999). During weekly pinniped surveys from the lighthouse, fur seals were counted and their age, sex, and location were recorded. However, the location of the northern fur seal breeding colony on West End Island is not entirely visible from the lighthouse, so after active northern fur seal breeding was first observed there in 1996, one or more visits each year were made to the breeding site to conduct a ground-based count and read flipper tags. One visit per year was performed in 1996–2005 (except 1998) and 2012, with 2–9 visits conducted during all other years (mean = 3.4 surveys per year). Ground survey dates ranged from 12 August to 28 November, with a mean survey date of 1 October.

Ground count data should be regarded as a minimum index of abundance rather than a precise indicator of the pup population for several reasons: 1) ground counts are incomplete because researchers do not enter breeding areas until the end of the pupping season in order to reduce human disturbance; 2) pup mortality occurring prior to the count is not accounted for; and 3) by the time ground counts are conducted, many pups have learned to swim and may not be present at the rookery. Additionally, yearlings may be present at rookeries and can be misidentified as pups. To correct for some of these biases in South Farallon Islands ground counts, aerial photographic surveys of the colony were conducted during 2013–2016. A correction factor was then calculated to correct for the proportion of pups missed during standard ground-based surveys. Pup-count data used in this study for the South Farallon Islands from 1996 to 2012 were annual maximums from ground surveys corrected using the mean correction factor estimated from aerial surveys (corrected pup count = max pup count/0.336). Pup counts from aerial surveys were used from 2013 to 2016.

At Bogoslof Island, data were collected in July or August each year for 1 day in all years except 1997 (mean date = 11 August). From 1980 to 1995 data were collected by ground counts of pups made by walking through or near the breeding areas (Loughlin and Miller 1989; National Marine Fisheries Service's Fur Seal Investigations reports). In 1990 and 1994, counts of live and dead pups were combined, but in 1991, 1993, and 1995 dead pups were not counted. In 1997, from 4 to 23 August, live and dead pups were counted, and counts of live pups were adjusted for detectability by the shearing mark-recapture method (Chapman and Johnson 1968; Ream et al. 1999). Bogoslof Island counts are minimums because some pups were missed during counts before 1997, and dead pups were often not accounted for.

At San Miguel Island, data were collected May–September each year from a combination of ground counts consisting of daily observations of live and dead pups from a blind at Adam's Cove and 1 or a few counts at Castle Rock each year from the ground. Data for Castle Rock were also occasionally collected with aerial photographic surveys. Details of each year's methods are available in National Marine Fisheries Service's Fur Seal Investigations reports (1970–1985). Because the San Miguel Island colony was not detected until 40 pups were observed in 1968, and reliable sightings of adult northern fur seals were reported as early as 1965 (Peterson et al. 1968), we analyzed a data set that began with 1 pup in 1962 (a back-calculated estimate based on the South Farallon Islands growth curve), and actual pup counts from 1968 to 1982, to represent the first 21 years of colony growth at San Miguel Island for comparison with the South Farallons and Bogoslof Island.

Aerial surveys.—We conducted aerial photographic surveys of the South Farallon Islands colony during the first week of August each year (2013–2016) when annual pup numbers were expected to be near their peak. At the time of aerial surveys in the peak breeding season, pups spend very little time in the water (Baker and Donohue 2000), and the majority of females should have given birth (Temte 1985; Trites 1992; Trites and Antonelis 1994). Because of survey timing, photographs did not account for pup mortality very early in the breeding season, but mortality was low based on the number of carcasses seen in photographs.

Surveys were conducted in a fixed-wing, high-wing Partenavia PN68 aircraft (Aspen Helicopters, Inc., Oxnard, California). All coastlines and other pinniped breeding and haul-out areas of the South Farallon Islands were photographed from a height of 200–365 m above sea level, at a speed of 167 kph, and between 1300 and 1700 h. Two photographers took near-vertical handheld photographs through a belly port in the aircraft. The lead photographer took close-up photographs for counting with a Canon EOS 60D digital SLR camera and a 200 mm lens. The backup photographer took general overview photographs of pinniped haul-out areas for geographic reference with a Canon EOS 30D digital SLR camera and a 17–85 mm zoom lens. An observer kept a flight and photograph log.

We used Microsoft Office's Photo Gallery to create a panorama mosaic using all photographs of the breeding colony. The mosaic was uploaded into the iTag 0.7 software to count pups. Pups were easily distinguished by their very small size. We used pup counts from aerial surveys to create a correction factor for existing ground survey data, and aerial photos to map the spatial extent of the breeding colony.

Population growth.—Population growth rate (lambda) characterizes population change, and is a useful metric for managers and population biologists to compare population dynamics among sites (Eberhardt and Siniff 1977). We used 2 methods of analysis, a classical and a Bayesian approach, to estimate lambda. For both approaches, to determine if colonies had shifted from "recolonization" to "maturity" phases (Roux 1987), we used pup counts to estimate island-specific lambda for the first 10 and 21 years at each site for a total of 6 time

series of pup counts (Table 1). Colony age 1 was defined as the first year pups were detected (South Farallon Islands and Bogoslof Island), or the back-calculated first year of pupping (San Miguel Island), to compare population trajectories during the earliest years after (re)colonization.

For the classical approach, we estimated lambda using linear regression of the natural logarithm of annual pup counts versus age of colony. The exponential rate of increase r, is the slope of the regression line, and was converted as: lambda = e^r.

For the Bayesian approach, we used state-space models analyzed with Bayesian inference to estimate the average stochastic population growth rate (r_t) at each island. We converted r_t as: lambda = e^{r_t}. State-space models are hierarchical models that enable estimation of population parameters while accounting for both process variation and observation error, and that explicitly account for missing data (Kéry and Schaub 2012).

Change in population size over time was modeled as a Markovian process because population size in year $t + 1$ depends on population size in year t. Our state-process model was defined as $\log(N_{t+1}) = \log(N_t) + r_t$, with $r_t \sim N(\overline{r}, \sigma_r^2)$. We fit models using Markov chain Monte Carlo (MCMC) methods with JAGS 4.3.0 (Plummer 2013) software executed using the jags function of the jagsUI package in the R statistical computing environment (R Core Team 2017).

One advantage of the Bayesian approach for inference is that years with missing values, as on Bogoslof and San Miguel islands, could be explicitly included in the analysis since the missing data are simulated by the MCMC sampler during each update (Schmidt et al. 2009). The Bayesian approach treats parameters as random variables and requires that prior distributions be specified for each random variable. The MCMC procedure uses simulations that produce Markov chains that provide parameter estimates from their posterior distributions (Zimmerman et al. 2012).

We analyzed each island separately because the survey time periods did not overlap sufficiently to include year-specific effects. We defined a prior for initial population size at each site as the log of the first-year count (Kéry and Schaub 2012). The prior for the initial population size was modeled with a lognormal distribution, and the prior for mean lambda was modeled with a normal distribution. Priors for *SD*s of the state process and the observation error were modeled with uniform distributions. Sampling protocol differed between the periods 1996–2012 and 2013–2016 at the South Farallon Islands, so we designed the model to account for potentially different observation errors between these 2 periods (this resulted in more precise lambda estimates). We based estimates of posterior distributions of lambda, and *SD* of lambda, on 3 chains of 200,000 iterations after a burn-in of 100,000 samples of the Gibbs sampler with a thin rate of 6. We assumed successful convergence of the Markov chains was reached when the Gelman–Rubin diagnostic (r-hat) for each of the random variables was < 1.1. We plotted annual pup counts and the posterior means of population sizes along with 95% credible intervals.

We compared r and r_t among sites using z-tests. We computed: z-score = diff/*SE* for the diff; where diff = $r_a − r_b$; *SE* for the diff = $\sqrt{SE_a^2 + SE_b^2}$ (subscripts a and b refer to different islands). We expected all 3 sites to be in the early recolonizing phase of Roux (1987), with no evidence of density dependent effects nor slowing growth rates indicating maturity phase.

Age and sex structure.—We recorded all tagged individuals observed during ground counts at the South Farallon Islands from 2006 to 2016. We obtained information on natal colony, age, and sex for each individual tag sighting from the Marine Mammal Laboratory's database. Based on this information, we examined the age and sex distribution of immigrants. First reproduction in females may occur at 3 years of age, with means of 5–6 years of age (York 1983). Males may hold breeding territories as early as 7 years of age, but most breeding males are 10–13 years old (Johnson 1968; Vladimirov 1987). On the Pribilof Islands, natal site fidelity of northern fur seals is generally high, increases with age, and females are more likely to return to their natal site compared to males at every age (Baker et al. 1995). Furthermore, mortality rates are higher for immature females than immature males (Wickens and York 1997; Lee et al. 2014). Based on these studies indicating higher dispersal and higher survival rates for males versus females, we predicted the age and sex distribution of immigrants to the South Farallon Islands should be biased toward mostly males and possibly biased toward mostly younger ages.

Population recovery.—We explored how population growth rates of fur seals from sites and species around the world varied

Table 1.—Count data for northern fur seal (*Callorhinus ursinus*) pups at the South Farallon Islands, California, Bogoslof Island, Alaska, and San Miguel Island, California. ND indicates no data available. South Farallon Islands data from 1996 to 2012 are annual maximum counts from ground surveys, which have been adjusted using the mean correction factor derived from aerial surveys conducted from 2013 to 2016.

South Farallon Islands		Bogoslof Island		San Miguel Island	
Year	Pups	Year	Pups	Year	Pups
1996	3	1980	2	1962	1
1997	12	1981	ND	1963	ND
1998	3	1982	3	1964	ND
1999	9	1983	12	1965	ND
2000	12	1984	14	1966	ND
2001	15	1985	9	1967	ND
2002	39	1986	ND	1968	40
2003	24	1987	ND	1969	28
2004	33	1988	80	1970	33
2005	71	1989	99	1971	45
2006	288	1990	183	1972	165
2007	184	1991	413	1973	261
2008	187	1992	ND	1974	521
2009	229	1993	898	1975	725
2010	377	1994	1,472	1976	938
2011	505	1995	1,272	1977	1,038
2012	597	1996	ND	1978	1,168
2013	401	1997	5,096	1979	1,487
2014	656	1998	ND	1980	1,459
2015	665	1999	ND	1981	1,538
2016	1,126	2000	ND	1982	1,709

with time in comparison with the 4 stages of population recovery described by Roux (1987). We performed a literature search using Web of Science and Google Scholar to search for the terms "fur seal" and "population" and extracted records from the search results and from the references in publications found in the search. We extracted all records of positive population growth rates based on pup counts. Because we were interested in recovering populations only, we excluded populations in long-term decline, such as the Pribilof Island colonies of northern fur seals (Trites and Larkin 1989). For each record, we recorded the species, site, maximum pup population in the time series, start year, end year, and population growth rate as a percent increase per annum or a finite rate of population growth. Where many subsites were analyzed (e.g., many beaches on a single island), we used only the grand mean rate of growth for the entire island or population. We converted all growth rates to lambda for comparison. We assembled time series for species and sites with lambda estimates from ≥ 4 periods with periods of > 2 years.

We explored how population growth rate varied with time by examining x-y scatter plots of year growth rate using the midyear for the period of estimated growth and growth rate as lambda. We expected the relationship of lambda to time would be a positive quadratic relationship, reflecting a low initial population growth rate during the "survival" stage (lambda < 1.05), increased lambda in the middle periods during the "establishment" (lambda = 1.05–1.10) and "recolonization" (lambda > 1.10) phases, and lambda near 1.0 in later periods during the "maturity" phase (Roux 1987).

RESULTS

Colonization history and spatial extent.—The first modern record of northern fur seals on the South Farallon Islands was in 1964 when a female was collected near the future recolonization site at Indian Head on West End Island (Pyle et al. 2001; Fig. 1). Beginning in 1984, increasing numbers of northern fur seals were sighted at the recolonization site, and the first pup was sighted in 1996 (Pyle et al. 2001). Pups have been born every subsequent year, and the colony has expanded northwest up the sloping valley to cover an area of about 5,000 m² (Fig. 1). Another estimated 25,000 m² of area is available for colony expansion near the current colony and additional space of more than 50,000 m² is available across the entire South Farallon Islands.

The substrate of the recolonized breeding site is bare granite with a cobble beach in the intertidal zone, and above the tide line crumbling granitic spires are surrounded by talus slopes and flats covered with guano-cemented rocks with some scattered gravelly sand composed of crushed and weathered California mussel (*Mytilus californianus*) shell fragments. Some upper slopes are covered with vegetation during the winter months, mostly maritime goldfields (*Lasthenia maritima*).

Population growth.—The northern fur seal population on the South Farallon Islands has increased rapidly since recolonization at 34% per year over 21 years (Table 2; Supplementary

Data SD1). However, all 3 islands had different 21-year growth rates: Bogoslof Island had the fastest growth rate, at 59% mean annual percent growth in pup numbers; San Miguel Island had the second fastest, at 45% mean annual percent growth in pup numbers; and the South Farallon Islands had the slowest (Fig. 2; Table 2; South Farallon Islands – Bogoslof Island: $z = 6.38$, $P < 0.001$; Bogoslof Island – San Miguel Island: $z = -2.57$, $P = 0.005$; San Miguel Island – South Farallon Islands: $z = -2.24$, $P = 0.013$). The 10- and 21-year mean growth rates did not differ on any individual colony (Fig. 2), indicating 2 decades of steady growth at all 3 sites. Results from classical analysis were similar to those obtained using Bayesian methods.

Age and sex structure.—Between 2006 and 2016, we made a total of 60 ground count visits to the South Farallon Islands colony, where 362 tag readings were recorded representing 203

Table 2.—Estimates of 21-year population growth rates of (re)colonized breeding colonies for northern fur seals (*Callorhinus ursinus*).

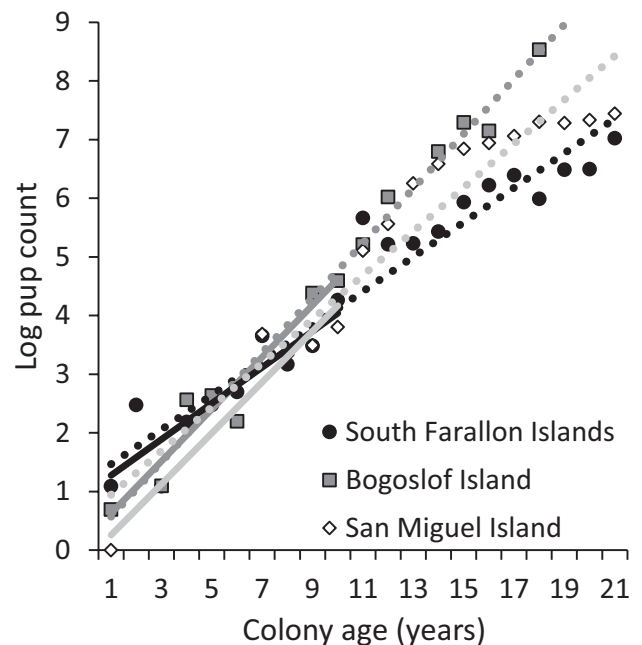|	South Farallon	San Miguel	Bogoslof
Location	California	California	Alaska
Years	1996–2016	1962–1982	1980–2000
21-year classical r	0.295	0.374	0.466
SE	0.019	0.030	0.019
21-year Bayesian r_t	0.287	0.373	0.463
SD	0.085	0.103	0.073
Classical lambda	1.343	1.454	1.594
Bayesian lambda	1.328	1.452	1.589

Fig. 2.—Natural logarithm of number of northern fur seal (*Callorhinus ursinus*) pups observed on the South Farallon Islands (black), Bogoslof Island (dark gray), and San Miguel Island (light gray) during the first 21 years of available pup counts post-(re)colonization. Solid lines are 10-year growth rates, dotted lines are 21-year growth rates. Ten-year growth rates did not differ from 21-year growth rates at any site. Twenty-one-year growth rates differed among all 3 sites.

unique animals. Based on tag type and color, almost all tagged animals observed at the South Farallon Islands originated from San Miguel Island, except for 1 sighting of an immature animal from the Commander Islands, Russia. The age of most immigrants to the South Farallon Islands from San Miguel Island was 3 or 4 years old when they were first sighted, with the median age 4 years for both females and males (Fig. 3; females: mean = 4.6, range 1–13; males: mean = 4.2, range 2–11). The 203 tagged immigrants had an equal sex ratio overall (m:f = 100:103), and within each age class for ages 2–6 (2 = 15:13, 3 = 24:26, 4 = 26:21, 5 = 12:13, 6 = 14:10), but was slightly female-biased for ages > 6 (9:19).

Population recovery.—We assembled 71 records of population growth rate based on pup-count data for 8 species of fur seal at 32 sites (Supplementary Data SD2). We found 6 sites representing 3 species with lambda estimates from 4 or more time periods (mean number of time periods = 5.8, range = 5–7). Six of the 7 populations exhibited the positive quadratic trend that we expected to find, describing population recovery over time (Fig. 4) with the quadratic trend lines fitting the data reasonably well (mean adjusted $r^2 = 0.69$, SD = 0.17, excluding South Georgia Island). The South Georgia Island population of Antarctic fur seals (*Arctocephalus gazella*) had an inverse curve from what we expected. All sites except 1 had lambda values > 1.10 at some point during their time span, indicating the sites were in the "recolonization" phase. The one species that never exhibited lambda > 1.10 (Roux's (1987) definition of the recovery phase) was the Australian fur seal (*Arctocephalus pusillus doriferus*).

DISCUSSION

The first 2 decades of the recolonized northern fur seal breeding site at the South Farallon Islands can be characterized as a
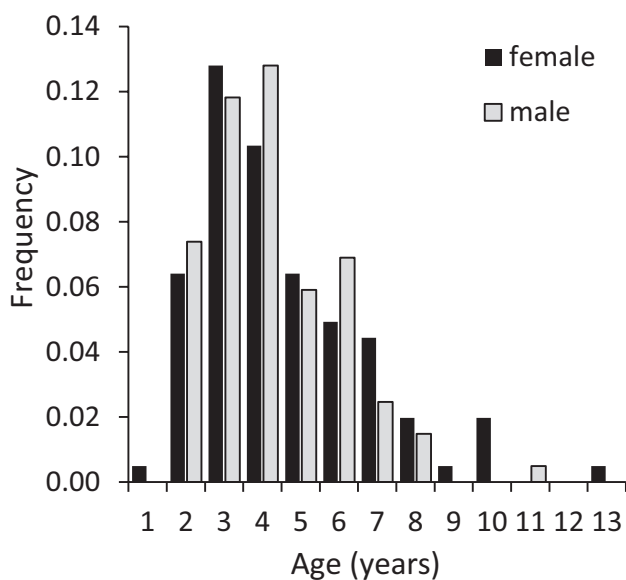

Fig. 3.—Age and sex distribution of tagged northern fur seals (*Callorhinus ursinus*) from San Miguel Island that immigrated to the South Farallon Islands, 2006–2016. Ages are age at arrival (first tag reading). *n* = 203 unique animals.

period of steady population growth and geographic expansion. Populations at all 3 islands considered here grew at very high rates during their first 21 years after (re)colonization (mean lambda = 1.46; Fig. 3), exhibiting rates near the upper range of population growth rates observed for fur seals worldwide (Supplementary Data SD2). Population growth was the highest at Bogoslof Island, followed by San Miguel Island, then the South Farallon Islands. Space is available for continued expansion on all 3 islands, although Bogoslof Island has been an active volcano during 2017 that may change available rookery habitat. Current overall populations documented at the South Farallon, San Miguel, and Bogoslof islands account for 0.2%, 0.9%, and 8.5% of the world's northern fur seal population, respectively (Gelatt et al. 2015). If the South Farallon Islands population reaches its estimated historical size of 100,000 individuals (Starks 1922; Townsend 1931; Scheffer and Kraus 1964), it could account for approximately one-fifth of the world's northern fur seal population.

Fitness benefits should exist in (re)colonized sites for individuals to be attracted there and to succeed in their new habitat (Smith and Peacock 1990; Danchin et al. 1998; Kildaw et al. 2005). Northern fur seals occurred historically at breeding colonies on the South Farallon Islands, and prehistorically at breeding colonies on San Miguel Island and at many mainland sites (Jones and Hildebrandt 1995; Burton et al. 2001). However, the northern fur seals in California that were extirpated in the 1800s may have exhibited a different life history and foraging behavior compared to modern northern fur seals (Newsome et al. 2007). Continued high population growth rates and continuous immigration of tagged animals to all 3 islands in this study indicate that both the California Current and Bering Sea ecosystems have been providing adequate fitness benefits for northern fur seals breeding at these 3 colonies. This is in contrast to the Pribilof Island colony in the Bering Sea, which is in long-term decline (Trites and Larkin 1989). The possibility remains that the new colonies could be population sinks that are sustained only by immigration from other sites (Lidicker 1975; Pulliam 1988), but a metapopulation model indicated immigration only sustained population growth during the first 8 years after (re)colonization, with intrinsic population processes maintaining growth thereafter (Lee et al. 2014).

Immigration is clearly ongoing at the South Farallon Islands, as shown by the tagged individuals from San Miguel Island arriving each year. There may also be immigrants from other colonies, but because animals are not tagged regularly (or at all) at some colonies, we cannot be sure of the true provenance of all immigrants to the South Farallon Islands. The age distribution immigrants to the South Farallon Islands that were tagged on San Miguel Island was skewed towards the younger age classes relative to the age distribution of tagged animals sighted at San Miguel Island (Testa 2008, 2011, 2012, 2013, 2016). This age skew is expected, as younger animals are more likely to disperse (Baker et al. 1995). However, the sex ratio of animals tagged and resighted at their natal colony on San Miguel Island was male-biased in the 2-, 3-, and 4-year-old age classes (e.g., figure 20 in Testa 2016), whereas the sex ratio was
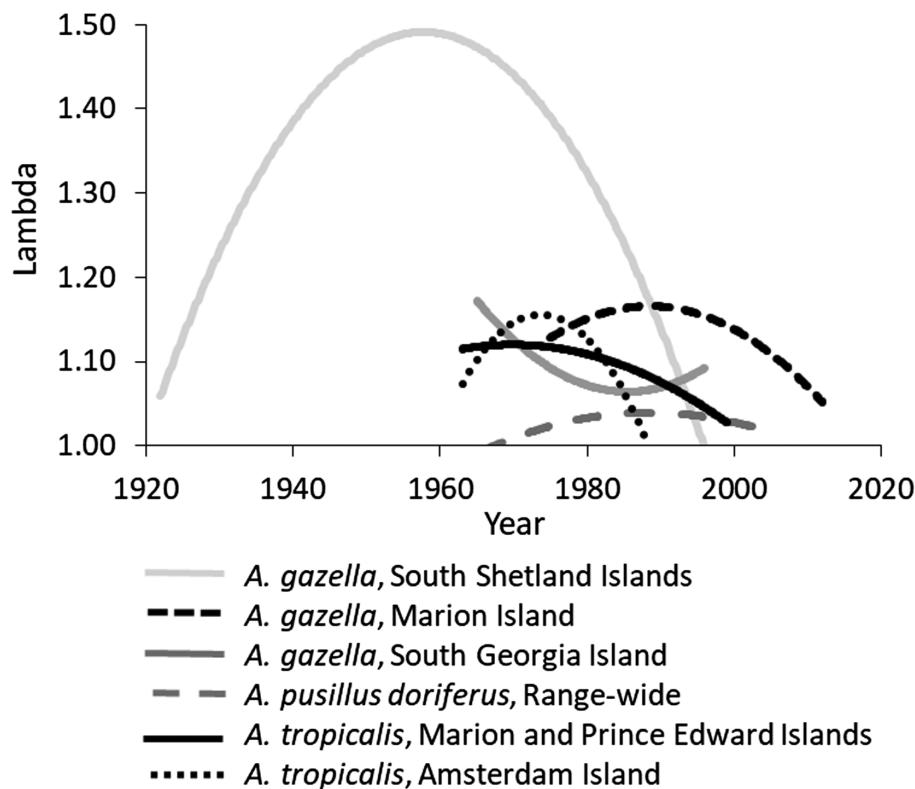
Fig. 4.—Lambda (population growth rate) over time for 7 recovering fur seal (*Arctocephalus* spp.) populations. The positive quadratic relationship reflects a low initial population growth rate during the "survival" stage, increased lambda in the middle periods during the "establishment" and "recolonization" phases, and lower lambda again in later periods during the "maturity" phase (sensu Roux 1987). Lamda values for various periods are presented in Supplementary Data SD2.

nearly equal among immigrants in every age class at the South Farallon Islands (Fig. 3). The sex ratio of northern fur seals is equal at birth, becomes male-biased in young animals, and female-biased after age 8 due to sex differences in age-specific survival rates (Wickens and York 1997; Lee et al. 2014). These age-related sex-ratio biases were observed among site-faithful tagged animals at San Miguel Island, so the observed equal sex ratio among young fur seals at the South Farallon Islands indicates a deviation from the underlying sex distribution of tagged animals. This deviation is evidence that young females are more likely than young males to make prospecting trips to the South Farallon Islands from their natal colony at San Miguel Island. This behavior appears to differ from the site fidelity patterns described for this species in the Bering Sea (Baker et al. 1995). Because data were not collected on the breeding status of tagged animals sighted at the South Farallon Islands, further study is required to determine the ontogeny of prospecting and breeding behavior of immigrating fur seals at the South Farallon Islands relative to the animals that breed at their natal colony (Reed et al. 1999; Clobert et al. 2009; Delgado et al. 2014).

The San Miguel Island population's growth rate has been substantially affected by strong ENSO events, when the population experiences reduced reproductive success and high mortality of pups and adults (Hickey 1979; DeLong and Antonelis 1991; Melin et al. 2008), and we expected the South Farallon Islands population to be similarly affected. The South Farallon

Islands experienced the very strong 1997–1998 ENSO event and showed a 75% decline in pup numbers, and also experienced the weak 2006–2007 ENSO event that resulted in a 36% decline in pup numbers. ENSO events appear to be impacting both the South Farallon Islands and San Miguel Island populations, which may partially explain their lower population growth rates compared to Bogoslof Island.

The difference in population growth rates between the South Farallon Islands and San Miguel Island could be attributable to the different topography at these 2 colonies. At the South Farallon Islands, the colony breeds on a steep rocky slope with only a small area where animals can enter and leave the sea, whereas at San Miguel Island, animals breed on a large, gently sloping sandy beach and rocky islet (Peterson et al. 1968). The colony at Bogoslof Island is among large boulders adjacent to a sandy beach (Loughlin and Miller 1989). Differences in the colonies' accessibility from the sea to breeding sites on land or availability of territorial space could also influence immigration or recruitment rates and thus the population growth rates.

Another difference between the San Miguel Island and South Farallon Islands populations may be disease. Aerial photos indicated that pup mortality on the South Farallon Islands appears to be low, with only 5 dead pups detected over the past 4 years (0.2% mortality). This is in stark contrast to San Miguel Island, where annual pup mortality currently ranges from 5% to 64%, with hookworm disease (*Uncinaria* sp.) implicated in 95% of the dead pups < 1 month old (Lyons et al. 2001; Melin et al.

2008). It is possible some aspect of the South Farallon Islands colony is inhibiting hookworm disease there (DeLong 2007).

Our examination of the temporal changes in population growth rates for fur seals around the world during their recovery processes indicated that the general framework described by Roux (1987) is an effective description of fur seal population recovery. The one exception to the pattern was the Australian fur seals in Bass Strait. As fur seal populations approach carrying capacity, we have an opportunity to examine the specific demographic changes that cause the slowdown in population growth (Eberhardt 2002). Understanding these demographic processes has implications for conservation of marine mammal species that are not yet recovering (Meyer et al. 2015).

SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.
Supplementary Data SD1.—Figures showing counts (black dashed lines) and estimated population size (gray lines) of northern fur seal (*Callhorinus ursinus*) populations at South Farallon Island (SFI) and San Miguel Island (SMI), California, and Bogoslof Island, Alaska (BI), with 95% credible interval (CRI) (shaded).
Supplementary Data SD2.—Table of population growth rates for fur seals used in analysis of population recovery patterns.

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