Population status, seasonal variation in abundance, and long-term population trends of Steller sea lions (*Eumetopias jubatus*) at the South Farallon Islands, California*

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Abstract—We examined seasonal and annual variation in numbers of Steller (northern) sea lions (*Eumetopias jubatus*) at the South Farallon Islands from counts conducted weekly from 1974 to 1996. Numbers of adult and subadult males peaked during the breeding season (May–July), whereas numbers of adult females and immature individuals peaked during the breeding season and from late fall through early winter (September–December). The seasonal pattern varied significantly among years for all sexes and age classes. From 1977 to 1996, numbers present during the breeding season decreased by 5.9% per year for adult females and increased by 1.9% per year for subadult males. No trend in numbers of adult males was detected. Numbers of immature individuals also declined by 4.5% per year during the breeding season but increased by 5.0% per year from late fall through early winter. Maximum number of pups counted declined significantly through time, although few pups were produced at the South Farallon Islands. The ratio of adult females to adult males averaged 5.2:1 and declined significantly with each year, whereas no trend in the ratio of pups to adult females was discernible. Further studies are needed to determine if reduced numbers of adult females in recent years have resulted from reduced survival of juvenile or adult females or from changes in the geographic distribution of females.

Steller sea lions (*Eumetopias jubatus*) range from southern California along the West Coast of North America through the Aleutian and Pribilof Islands to the Kuril Islands and Okhotsk Sea, Japan (Kenyon and Rice, 1961). Major haulouts and rookeries have historically been centered at the Aleutian Islands and at islands and mainland sites around the Gulf of Alaska, where over 70% of the world population was located in the 1950s and 1960s (Loughlin et al., 1984). In 1990, the species was listed as threatened throughout its range under the Endangered Species Act owing to declines of over 50% from an estimated world population of 240,000–300,000 in the early 1960s to 116,000 individuals in 1989 (Loughlin et al., 1992). Numerically the decline was most severe in the western Gulf of Alaska where 50–80% declines occurred (Loughlin et al., 1992). Reduced juvenile survival appears to be the proximate cause for the decline (York, 1994); ultimate causes, however, are unknown. Effects of long-term environmental change and pollutants on Steller sea lions, and interactions or competition of these sea lions with commercial fisheries are potential contributing causes of this decline (NMML[1]).

In contrast to rookeries in the western Gulf of Alaska, southeast Alaska rookeries have increased by more than 60% over the past three decades (Loughlin et al., 1992). Based on differences in population trends and genetics (Bickham et al., 1996), a distinction has been made between two separate stocks: 1) the eastern stock, ranging from southeast Alaska to California, and 2) the western stock, ranging from the Gulf of Alaska, Aleutian Islands, and Pribilof Islands to Russia (U.S. Federal Register 62:24345–24355). In 1997, the National Marine Fisheries Service listed the western stock as endangered, whereas the eastern stock remained listed as threatened. However, differences in trends between rookeries in southeast Alaska and those in Canada, Oregon, and California may indicate that these areas deserve separate management considerations.

For example, rookeries in Canada and California suffered 40% and 80% declines respectively, from the early 1900s to 1970 (Bigg, 1988; Ainley et al.[2]); declines continued over the past
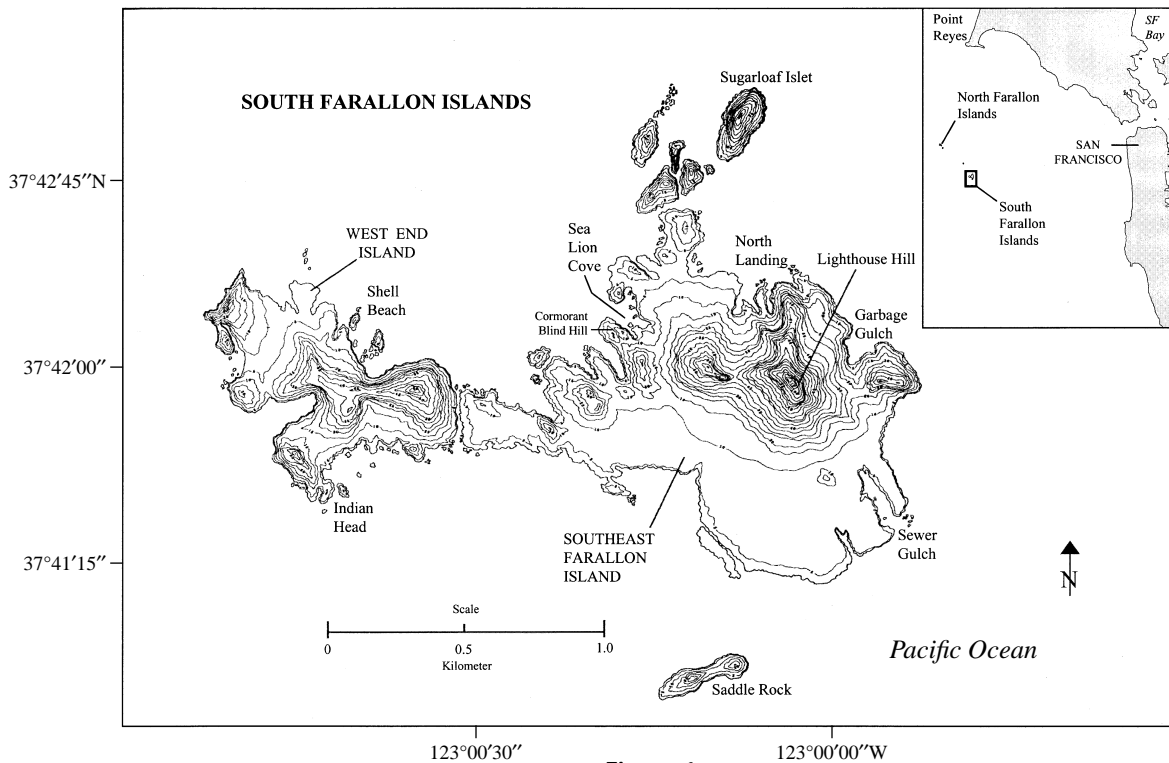
Figure 1

Map of the South Farallon Islands, including Southeast Farallon Island and West End Island. Steller sea lions were counted weekly from 1974 to 1997 from Lighthouse Hill, and several ground areas: North Landing, Cormorant Blind Hill, Sewer Gulch, and Garbage Gulch.

several decades at several California rookeries (Westlake et al., 1997; Sydeman and Allen, 1999; Le Boeuf et al.[3]). Whereas over 2000 Steller sea lions used the Channel Islands in the late 1930s, only 50 animals were observed there in 1959 (Bartholomew and Boolootian, 1960). Pupping at San Miguel Island, an historical rookery, has not been observed since 1981 (NMML[1]). Therefore to better understand patterns and causes of the population decline, trends and status of the eastern stock at southern rookeries deserve further investigation.

The Farallon Islands (37°42′N, 123°00′W), 40 km off the coast of San Francisco, California, are currently one of the most southerly haulout and breeding areas for Steller sea lions; Año Nuevo Island is the only rookery farther south. The Farallon Islands consist of three groups of islands: South Farallones (two islands, Southeast Farallon and West End, separated by a small surge channel), Middle Farallon (an intertidal rock), and North Farallones (four large sea stacks; Fig. 1). Although the status of Steller sea lions in California prior to 1800 was poorly documented, Steller sea lions bred at the Farallon Islands in the 1800s

and early 1900s (Allen, 1880; Rowley, 1929) and were the most abundant sea lion in California and at the Farallon Islands from the early to mid 1900s (Rowley, 1929; Bonnot and Ripley, 1948). A large amount of data is now available to examine seasonal variation and long-term trends at the Farallon Islands from historical surveys conducted from 1927 to 1970 by the California Department of Fish and Game (CDFG; Bonnot and Ripley, 1948; Ripley et al., 1962; Carlisle and Aplin, 1971) and from surveys conducted weekly by Point Reyes Bird Observatory (PRBO) from 1971 to 1996. Although maximum numbers declined significantly from 1974 to 1997 for the total population (1.6% per year) and for adult females (3.6% per year; Sydeman and Allen, 1999), it is unknown whether numbers of other age classes also declined and in which seasons declines occurred. To understand proximate causes and consequences of the decline, several questions have yet to be addressed: have reduced pup production and reduced reproductive rates also occurred in recent years?; and what effect has the decline had on the adult sex-ratio? Finally, seasonal variation in counts for different sexes and age classes and variation in the seasonal pattern among years also have not been examined in detail at the Farallon Islands. The objectives of our study were to examine 1) seasonal variation in numbers among sexes and age classes; 2) trends in numbers from 1974 to 1996 by age class, sex, and season; and 3) averages and trends in pup production, reproductive rate, and adult sex-ratio.

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[3] Le Boeuf, B. J., K. A. Ono, and J. Reiter. 1991. History of the Steller sea lion population at Año Nuevo Island, 1961–1991. Final report to National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, CA. Admin. report LJ9145C, 9 p. [Available from National Marine Fisheries Service, Southwest Fisheries Science Center, P.O. Box 271, La Jolla, CA 92038.]

Methods

Survey methods

PRBO began conducting surveys of pinnipeds at the South Farallon Islands in 1971. In June 1973 surveys were standardized and all Steller sea lions visible on or in the water near the coast of the South Farallon Islands were counted weekly from standard vantage points on Southeast Farallon Island: 1) atop Lighthouse Hill (110 m) with binoculars or a 20–60× spotting scope, 2) from Cormorant Blind Hill (35 m) with binoculars, and 3) from North Landing, Sewer Gulch, and Garbage Gulch with no optical aids (Fig. 1). Most surveys were conducted between 1000 and 1800 hours on Thursdays if visibility was adequate. Beginning in 1977, animals were classified by age class (adult male, subadult male, adult female, immature, yearling, or pup) when possible, primarily by body size. Adult males were distinctive as very large animals with large muscular necks bearing well-developed manes of long, coarse hair on the chest, shoulders, and back. Subadult males were distinguished from adult males by their smaller size and less developed mane. Immature individuals included animals of distinctly smaller size, such as young-of-the-year (after November) and animals likely one to four years of age. The adult female category included animals smaller than subadult males but larger than immature individuals. Pups were distinguishable from June until late November by their thick, dark brown coats, which were later molted and replaced with a lighter brown coat after five to six months of age. Counts were conducted by numerous observers over the years; several observers conducted surveys for over a decade and all observers were trained in identification of sea lions by age class. Counts represent minimum estimates of numbers of sea lions hauled out because only 85% to 90% of the islands were visible from the study's vantage points.

We compared maximum counts taken during the breeding season (June–July) in recent years (1974–97) with counts from surveys conducted a single time during the breeding season (once annually) and intermittently over the years by CDFG from 1927 to 1970. From 1927 to 1938, counts of subadult or adult sea lions (i.e. excluding pups) made by at least two observers from boats were averaged (Bonnot, 1931, 1937; Bonnot et al., 1938). Methods of counting changed after 1938, such that counts after 1938 could only be compared cautiously with earlier years. Surveys were conducted by airplane, blimp, or boat in 1946 and 1947 and by airplane only from 1958 to 1970 (Bonnot and Ripley, 1948; Ripley et al., 1962; Carlisle and Aplin, 1971). Counts from 1946 to 1970 were likely overestimates because observers assumed that all sea lions north of Point Conception were Steller sea lions (many sea lions may have been California sea lions, *Zalophus californianus*) and because pups were likely included in these counts (Bonnot and Ripley, 1948; Ripley et al., 1962). Counts conducted by PRBO since the 1970s targeted only the South Farallon Islands, whereas CDFG counts included the South and North Farallon Islands. Monitoring of the North Farallon Islands since 1970, however, has been sparse. Although the North Farallon Islands are a known haulout area for Steller sea lions, pupping rates are unknown. The North Farallon Islands were surveyed during the breeding season by PRBO in 1977 (when 17 adult females and 1 pup were counted) and in 1983 (when 92 adults but no pups were counted; PRBO, unpubl. data[4]). Because of the exclusion of the North Farallon Islands in recent counts, comparisons with earlier CDFG data were made cautiously.

Under the direction of D. G. Ainley and H. R. Huber, pup production and pup mortality were monitored intensively from 1973 to 1986, when animals were breeding in accessible areas. Breeding areas were checked daily for new pups, and prematurely born and dead pups were noted. Breeding areas shifted from accessible to inaccessible areas over the years. From 1973 to 1975, all full-term pups were born on the more accessible Saddle Rock, a small islet one-quarter mile offshore (Fig. 1), and a few premature pups were born on the mainland. From 1976 to 1983, females pupped in the equally accessible Sea Lion Cove (Fig. 1), perhaps because of reduced disturbance on Southeast Farallon Island, although one pup was observed on Saddle Rock in 1981. Although photographs from the 1930s show large numbers of Steller sea lions on West End (Huber[5]), they were not observed there in recent years until 1983 (one female in the spring). The first pup was born on West End in 1985 (Huber[5]). Currently, the majority of the population is found and all pupping occurs at Indian Head and Shell Beach on West End (Fig. 1); both of these areas are inaccessible and difficult to monitor.

Statistical analyses

Statistical models have been developed that account for effects of observer, and environmental and survey-related covariates on counts of birds and marine mammals (Link and Sauer, 1997, 1998; Calkins et al., 1999; Frost et al., 1999; Forney, 2000). These models can increase accuracy in estimating and power in detecting population trends by reducing variability in counts and correcting biases in trend that result from methodological changes in survey design over time (such as changes in survey dates), particularly when few surveys are conducted during a standard survey window each year (Calkins et al., 1999; Frost et al., 1999). However, environmental covariates could not be included in the statistical models in our study when the full data set was used because observers recorded the times that surveys began and ended on only a few occasions prior to 1983 (41 of 569 surveys, or 7.2% of surveys), such that the majority of data during the first decade of the time series would be excluded. To include the entire

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[4] PRBO (Point Reyes Bird Observatory). 1988. Unpubl. data. [Available from W. J. Sydeman, Point Reyes Bird Observatory, 4990 Shoreline Hwy, Stinson Beach, CA 94970.]

[5] Huber, H. R. 1985. Reproduction in northern sea lions on Southeast Farallon Island, 1973–1985. Final report to the Gulf of the Farallones National Marine Sanctuary, San Francisco, CA, 22 p. [Available from Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.]

time series, standard regression models, including survey date but excluding effects of environmental covariates, were used to examine seasonal patterns and trends. We believe the exclusion of other covariates during statistical modeling had little effect on trend estimates because surveys were conducted consistently over years and over the entire year interval, resulting in large sample sizes (n=1134 surveys conducted; range among years 1974–96: 45 to 52 surveys/year). It is unlikely that population trend estimates were confounded by changes in environmental conditions because no obvious annual trends in environmental conditions over the 22 years of the study (weather and tide data were collected daily [at 1000 hours] at Southeast Farallon Island) were apparent, except for a potential increasing annual trend in sea surface temperature (PRBO, unpubl. data[4]).

Seasonal abundance patterns   To examine seasonal abundance patterns, polynomial regression (Kleinbaum et al., 1988) was used to fit a curve to counts pooled over years, 1974 to 1996. Data from 1971 to 1973 were excluded because survey methods were not standardized until the end of 1973. We fitted the regression model by first converting Julian date to orthogonal polynomial variables (linear combinations of the natural polynomial variables that contain the same information as the natural polynomial variables but are uncorrelated to each other) to avoid problems of multicollinearity when using higher-order terms (Kleinbaum et al., 1988). Higher-order terms were then added sequentially until the last term was not significant in the model (forward stepwise procedure, P>0.05). We then added *year* as a variable to the model and tested the *year × date* interaction to determine if the seasonal pattern varied significantly among years. To examine seasonal patterns by sex and age class, polynomial regression curves were fitted separately to counts of adult females, males (adults and subadults pooled), and immature individuals as described above. We excluded surveys in which not all individuals were identified by sex and age class (i.e. all surveys before 1977).

Annual abundance trends   Because high-order polynomial models were used to address seasonal haulout patterns, annual abundance trends were examined in a separate analysis to simplify results. Seasonal variability in abundance was accounted for in annual trend models by using residuals from the regression of *Julian date* on counts. Assuming exponential rates of change, we log-transformed ($\log_e$) the residuals (centered about the mean count) and regressed the transformed residuals against the variable *year*. Annual rates of change were calculated as $e^{\beta_{Year}} - 1 \times 100\%$, where β_{Year} is the regression coefficient for annual trend (Caughley, 1977). The following groups were analyzed: 1) all animals, by pooling data over all 12 months and sex and age classes; and 2) each sex and age class, by pooling over a) all months, and b) two periods when peaks in counts were observed for some age classes (the breeding [May–July] and late fall through early winter [September–December] seasons). Nonlinearity in trend was assessed by using orthogonal polynomials as described earlier in this article. Assumptions of the regression model were verified by visual inspection of residuals.

Trends in pup production, reproductive rate, and adult sex ratio during the breeding season   We used linear regression to test if the decline in maximum pup counts during surveys presented in Sydeman and Allen (1999) was significant. We used only data after 1977, when counts by age class were conducted consistently. Only data from surveys conducted from June to July were included because during the fall, the ability to distinguish young-of-the year from immature individuals was difficult and because an influx of nonnative pups may have occurred. For example, in November 1978, five times the number of pups known to have survived the breeding season and an increased number of adult females were observed (PRBO, unpubl. data[4]). The origin of these young-of-the-year is unknown, but the nearest known pupping areas are Año Nuevo Island and the North Farallon Islands. Although Steller sea lions are present at Point Reyes, no pups have been observed there in the past two decades (Sydeman and Allen, 1999).
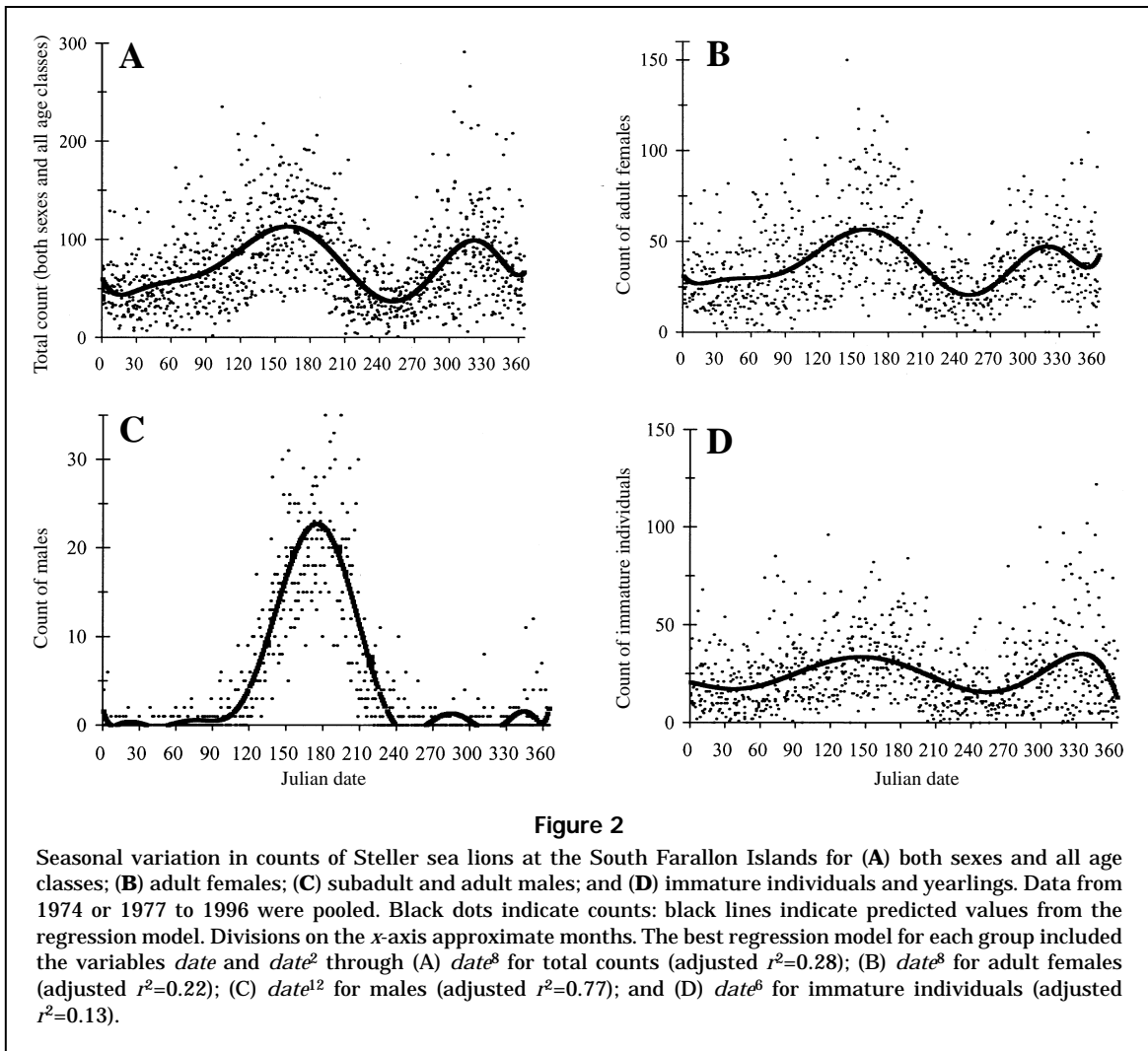
To examine averages and trends in adult sex ratio and reproductive rate, we used maximum counts of adult females, adult males, and pups during June and July in each year and linear regression to test for annual trends. Reproductive rate was calculated as the maximum count of pups divided by maximum count of adult females. Because not all pups born were observed during surveys, we increased the maximum count of pups by 57%, the average amount that maximum pup counts underestimated true pup production from 1973 to 1986 (range: 33–90% among years). This average was determined from unpublished data of pup production as determined from daily observations of breeding areas (Huber et al.[6]).

Results

Seasonal abundance patterns

When data from all sexes and age classes were pooled, the seasonal abundance pattern was bimodal; one peak in numbers occurred before and during the breeding season (April–July) and another peak occurred from late fall through early winter (October–December; Fig. 2A). The regression model was complex with significant date and higher-order terms (variables $date^2$ through $date^8$); all P<0.001; adjusted r^2=0.28, n=1134); the variable $date^9$ was not significant (P>0.65). Counts varied significantly with year (P<0.001) and the seasonal pattern varied significantly among years ($date \times year$ through $date^8 \times year$; P<0.001; adjusted r^2=0.61). Total numbers during the peak

[6] Huber, H. R., D. G. Ainley, R. J. Boekelheide, R. P. Henderson, and T. J. Lewis.   1988.   Annual and seasonal variation in numbers of pinnipeds on the Farallon Islands, California (Table 3).   Final report to the National Marine Mammal Laboratory, National Marine Fisheries Service, Seattle, WA, 35 p.   [Available from Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.]

Figure 2

Seasonal variation in counts of Steller sea lions at the South Farallon Islands for (**A**) both sexes and all age classes; (**B**) adult females; (**C**) subadult and adult males; and (**D**) immature individuals and yearlings. Data from 1974 or 1977 to 1996 were pooled. Black dots indicate counts: black lines indicate predicted values from the regression model. Divisions on the *x*-axis approximate months. The best regression model for each group included the variables *date* and *date²* through (A) *date⁸* for total counts (adjusted r^2=0.28); (B) *date⁸* for adult females (adjusted r^2=0.22); (C) *date¹²* for males (adjusted r^2=0.77); and (D) *date⁶* for immature individuals (adjusted r^2=0.13).

breeding season averaged approximately 100 animals, ranging from 50 to 200 animals; whereas numbers from the late fall through early winter peak were more variable, averaging slightly less than 100 and ranging from less than 10 to 300 animals (Fig. 2A).

Seasonal patterns varied among sexes and age classes (Fig. 2, B–D). Counts of adult and subadult males peaked only during the breeding season (Fig. 2C), whereas counts of adult females and immature sea lions were bimodal (Fig. 2, B and D). When models including the variables *date* through *date⁸* were fitted to data for adult females and immature individuals separately, the seasonal pattern differed significantly between the two groups *(age class, year,* and all interaction terms: all *P*<0.001). Counts of immature sea lions were less peaked during the breeding season than those of adult females and, in contrast to the average adult female pattern, numbers during winter peaked on average slightly higher than during the breeding season (Fig. 2, B and D).

The seasonal pattern varied significantly among years for all age classes (*year* and *year×date* interactions for adult females and immature individuals: *P*<0.001, and for subadult and adult males: *P*<0.05). Variation in seasonal pattern among years was complex but several general patterns could be noted. A gradual shift in the peak breeding season count from the beginning of May in 1974 to the beginning to middle of June in 1979 was evident (Hastings and Sydeman[7]). The late fall–winter peak was very pronounced from 1984 to 1986, with maximum counts of 200 to 300 animals (Hastings and Sydeman[7]), most of which were immature individuals. From 1992 to 1996, the seasonal abundance pattern was muted with equal or higher numbers in the winter than in the breeding season (Hastings and Sydeman[7]).

[7] Hastings, K. K., and W. J. Sydeman. 1998. Status, seasonal variation and long-term trends in numbers of Steller sea lions, *Eumetopias jubatus,* at the South Farallon Islands, California: 1927–1996. Final report to the National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, CA, 30 p. [Available from Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970.]

Table 1

Linear rates of change in counts of Steller sea lions on the South Farallon Islands by season, sex, and age class. Rate of change per year was calculated by 1) removing the effect of date on counts (i.e. by using residuals from regression of date on counts), and 2) log-transforming ($\log_e$) the sum of the residuals added to the mean count. * indicates significant trends ($P<0.05$) from regressions. n = sample size.

Age class	% change	β_{Year}	SE (β_{Year})	P	n
All animals					
All months	−0.44	−0.0044	0.0027	0.03*	1134
Adult females					
All months	−3.16	−0.0321	0.0032	<0.001*	866
Breeding season (May–Jul)	−5.89	−0.0607	0.0081	<0.001*	217
Late fall through early winter	2.50	0.0247	0.1637	0.80	280
Males (breeding season)					
All males	1.12	0.0111	0.0050	0.03*	217
Bulls	0.16	0.0016	0.0022	0.63	217
Subadult males	1.94	0.0192	0.0086	0.03*	217
Immature sea lions					
All months	0.55	0.0055	0.0019	0.004*	866
Breeding season	−4.51	−0.0461	0.0168	0.007*	217
Late fall through early winter	4.97	0.0485	0.0078	<0.001*	280

Annual abundance trends

Although visual inspection showed that residuals of log-transformed counts were not normally distributed, a square-root transform of counts normalized residuals. We report trend estimates from log-transformed counts because results of statistical tests for trends with log- and square-root-transformed data were identical.

After removing seasonal effects (i.e. residuals from regression of *date* on count were used), all sexes and age classes showed significant trends but in different directions (Table 1). When data from all sexes and age classes were pooled, the trend was complex (variables *year* through *year*³: all $P<0.05$; $n=1134$; Fig. 3A). Counts were highest in the late 1970s to early 1980s and declined only slightly during the late 1980s to early 1990s. A slight (−0.4% per year) linear decrease in total counts (pooling over months, sexes, and age classes) with *year* was significant ($P<0.05$; Table 1). Adult female counts declined significantly although the rate of decline slowed in recent years (variables *year* and *year*²: $P<0.01$; $n=866$; Fig. 3B). Counts of adult females declined significantly during the breeding season (variables *year* and *year*²: $P<0.01$; $n=217$; Fig. 3B), whereas no trend during late fall and early winter was evident ($P=0.80$; Table 1). Linear rate of decline for adult females was −3.2% per year for all months combined and −5.9% per year during the breeding season (both $P<0.001$; Table 1).

In contrast, numbers of males during the breeding season increased linearly with *year* at a rate of 1.1% per year ($P<0.05$; $n=217$; Table 1). This increase was due to an increased number of subadult males (1.9% per year; $P<0.05$; Table 1; Fig. 3C), whereas the numbers of adult males were stable ($P>0.60$; Table 1). Counts of immature indi-

viduals also increased slightly (0.6% per year; Table 1) but significantly when counts from all months were pooled (variables *year* and *year*²: $P<0.01$; $n=866$; Fig. 3D). The increase was due to the greater numbers of immature individuals from late fall through early winter in recent years (linear trend=5.0% per year, Table 1; *year* and *year*²: $P<0.01$; $n=280$; Fig. 4D). However, numbers of immature individuals present during the breeding season declined at a rate of −4.5% per year (Table 1; *year*: $P<0.01$; $n=217$; Fig. 3D).

Trends in pup production, reproductive rate, and adult sex ratio during the breeding season

Maximum pup count from surveys declined significantly from the mid-1970s to the mid-1980s from 15 to 2–4 pups and has remained low in recent years (*year* and *year*²: $P<0.003$; Fig. 4). After adjusting for pups not seen during surveys, reproductive rates of adult females ranged from 2.0% to 21.2% among years, with an average rate of 10.7% (Fig. 4). Although reproductive rate appeared to decline in the 1980s and recovered to 1970s levels in the 1990s, no trend was discernible (*year* and higher-order terms: $P>0.20$; Fig. 4). The ratio of adult females to adult males during the breeding season ranged among years from 10.3:1 to 1.8:1, with an average of 5.2:1 (Fig. 4). The ratio of adult females to adult males declined significantly and linearly with *year* ($P<0.001$).

Discussion

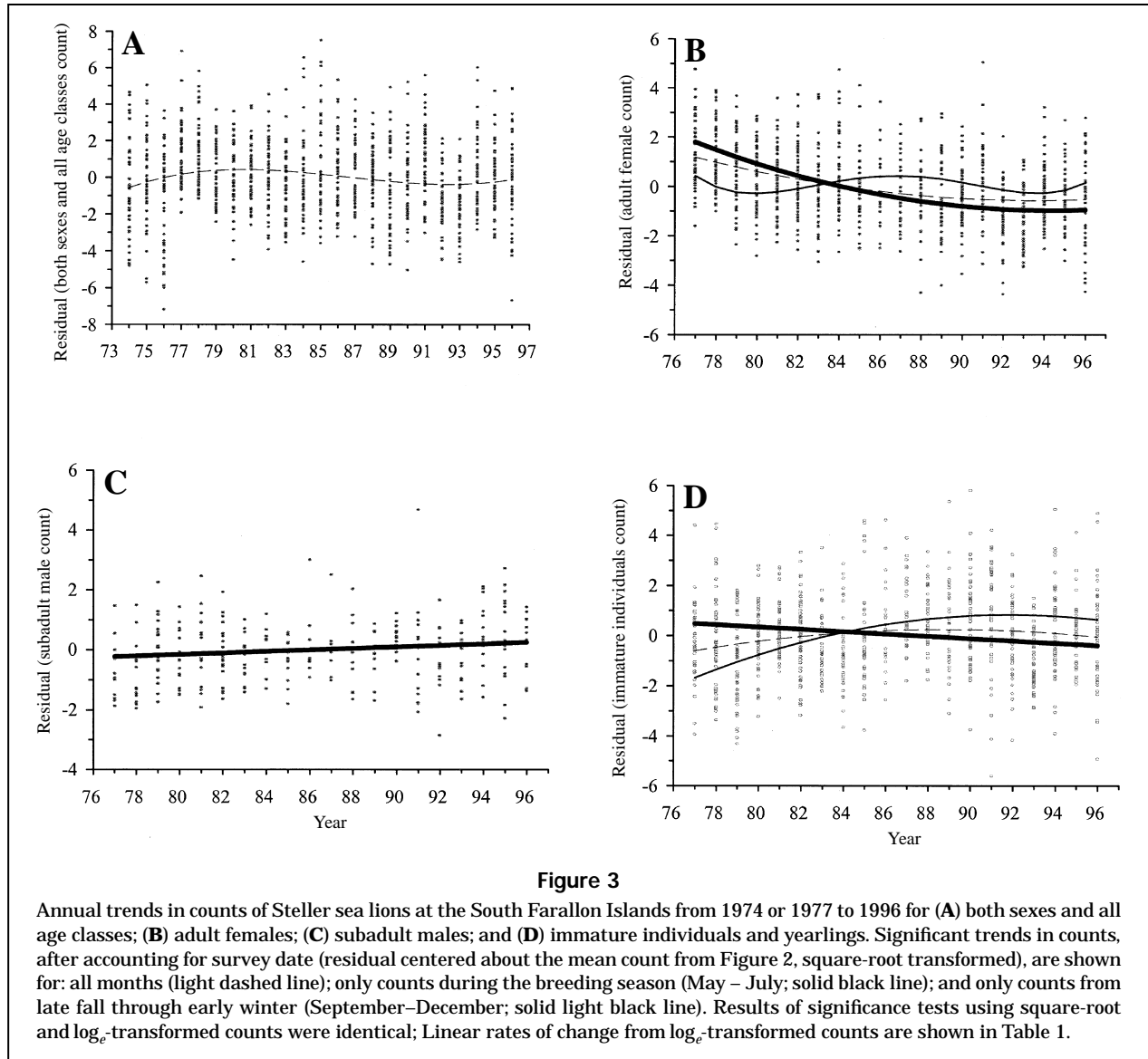Although the Farallon Islands are an important haulout area for Steller sea lions in California, numbers of ani-

Figure 3

Annual trends in counts of Steller sea lions at the South Farallon Islands from 1974 or 1977 to 1996 for (**A**) both sexes and all age classes; (**B**) adult females; (**C**) subadult males; and (**D**) immature individuals and yearlings. Significant trends in counts, after accounting for survey date (residual centered about the mean count from Figure 2, square-root transformed), are shown for: all months (light dashed line); only counts during the breeding season (May – July; solid black line); and only counts from late fall through early winter (September–December; solid light black line). Results of significance tests using square-root and $\log_e$-transformed counts were identical; Linear rates of change from $\log_e$-transformed counts are shown in Table 1.

mals at the Farallon Islands are currently lower (0.06 of the 1989 statewide count, 0.09 of the count from four major sites) than at the other three major California sites (Año Nuevo Island, St. George Reef, and Sugarloaf Island) which ranged from 0.16 to 0.18 of the 1989 statewide count, and from 0.26 to 0.37 of the count from four major sites (Loughlin et al., 1992). A smaller proportion of the statewide Steller sea lion population has used the Farallon Islands in recent years, compared with population counts in the 1927–30 data, when Farallon animals accounted for 0.11 to 0.14 of the statewide count (Bonnot and Ripley, 1948). Historical pup production at the Farallon Islands is unknown, but both the Farallon Islands and Año Nuevo Island were identified as the two largest and most important Steller sea lion rookeries in the state in the early 1920s (Rowley, 1929). Pup production at the South Farallon Islands over the past two decades has been very low at <30 pups per year and in the last 10 years, at <10

pups per year. Pup production since the mid-1980s, however, may be underestimated owing to the reduced probability of sighting pups since 1984 when pupping areas shifted to West End Island, which is farther away from the survey vantage points. Pup production at other major sites in California included 117–137 pups at Sugarloaf Island and Cape Mendocino in the early 1980s, 115 pups at St. George Reef in 1994, and 230–243 pups at Año Nuevo in 1993–94 (Westlake et al., 1997; NMML[1]).

Reproductive rates of Steller sea lions at the South Farallon Islands were also low; an average of only 0.11 of females present during the breeding season produced pups. This number may be biased low because some immature males may have been included in the adult female count. This ratio is much lower than that for rookeries in British Columbia (>0.70, Pike and Maxwell, 1958), Año Nuevo, California (average of 0.40 to 0.50 from 1962–1990; Le Boeuf et al.[3]) and Ugamak Island, Alaska, where ratio of

pups to females increased from 0.75 to >1.00 from 1968 to 1986 (Merrick et al., 1987). The South Farallon ratio is more typical of peripheral areas of rookeries in Alaska where only 0.01 to 0.09 of females had pups compared with main areas of rookeries where ratios averaged 0.63 to 0.74 (Withrow, 1982).

Similarly, high pup mortality rates observed at the Farallon Islands (average of 0.49 of pups born from February to August, range of 0.33 to 0.90 among years; Huber et al.[6]) are more characteristic of peripheral areas of rookeries where pup mortality ranged from 0.30 to 1.00 compared with 0.10 to 0.12 at main rookery sites (Withrow, 1982). Rookeries had much lower pup mortality rates during the first two months of life than those observed at the Farallon Islands, including Año Nuevo Island, California (0.10, Gentry, 1970), and sites in Alaska (0.03–0.14, Merrick et al., 1987). The frequency of premature pupping (0.40 of those born; Huber et al.[6]) is also very high compared with the frequency at rookeries in Alaska (0.09; Pitcher and Calkins, 1981), Oregon (0.04; Mate, 1973), at Año Nuevo Island (0.02; Gentry, 1970). As at Año Nuevo, most premature pups are born from February to May at the Farallon Islands (0.65 born in April with a range of February to May), whereas full-term pups are born from mid-May to late July (Gentry, 1970; Huber[5]). Causes of the high rate of premature pupping at the Farallon Islands are unknown but may be due to several factors known to cause reproductive failure in pinnipeds, including disease or exposure to pollutants (Gilmartin et al., 1976; Huber[5]), or a prevalence of young, inexperienced, or malnourished females (Pitcher et al., 1998). A high frequency of abortions has been observed at haulout sites rather than at rookeries in Alaska (Pitcher and Calkins, 1981). Low pup production and reproductive rates, coupled with high pup mortality and premature pupping rates, support characterization of the Farallon Islands in recent years as a haulout site or peripheral rookery for this species.

Seasonal patterns in counts

Seasonal haulout patterns varied significantly among sexes and age classes. Adult and subadult male attendance was highly seasonal and males were present only during the breeding season. In contrast, adult females and immature individuals were present year-round and their numbers peaked twice (breeding season and from late fall through early winter). Many studies reported the absence of adult and subadult males at California rookeries outside the breeding season, including Año Nuevo Island (Orr and Poulter, 1967) and San Miguel Island (Bartholomew, 1967), and the presence of females and immature individuals at rookeries year-round (Rowley, 1929; Bartholomew, 1967). At Canadian rookeries, males were also generally absent in the winter, but small numbers of females and young
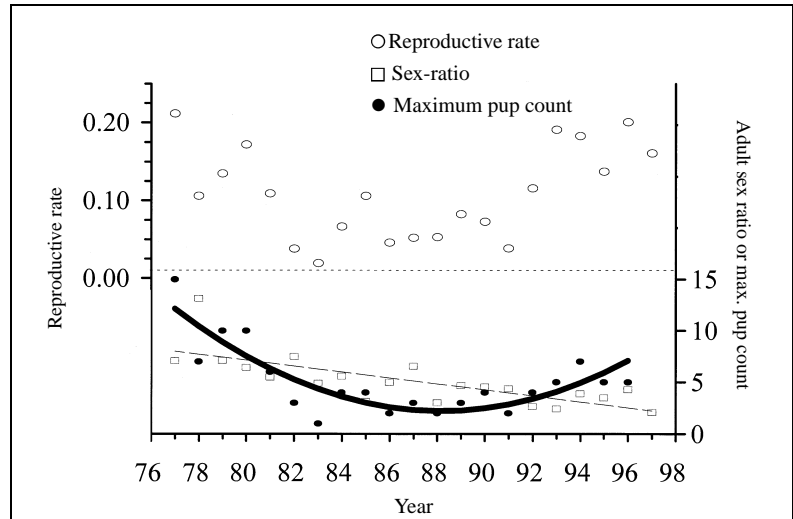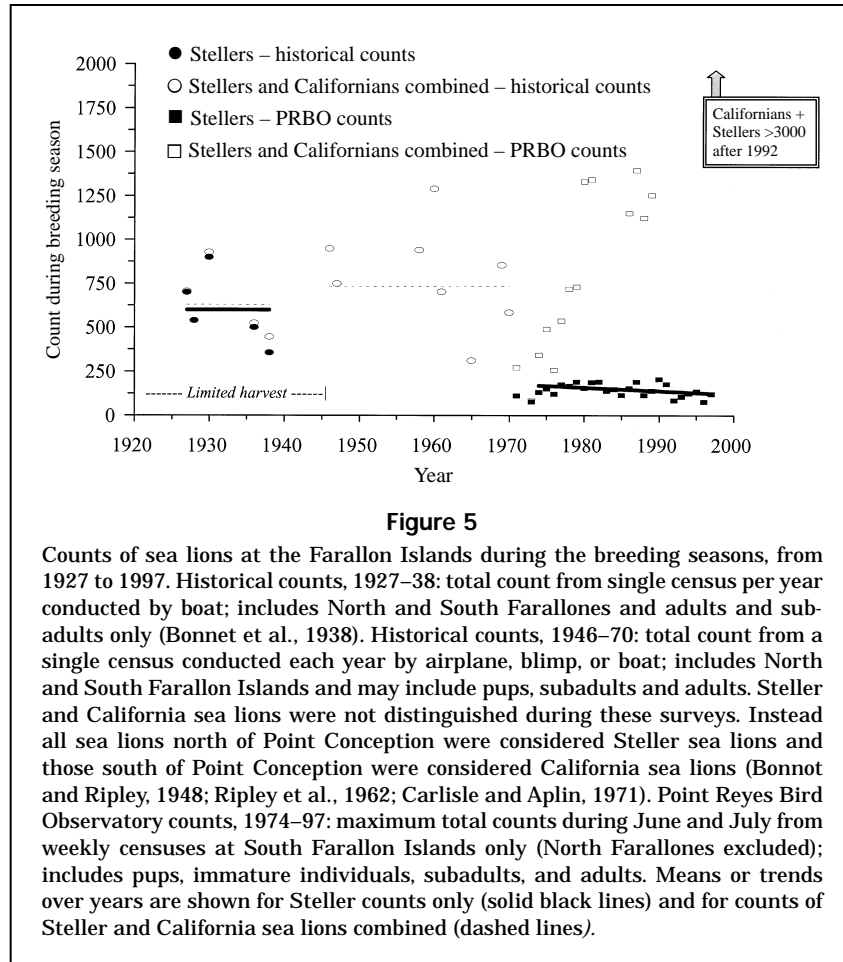

Figure 4

Annual variation in reproductive rate, adult sex ratio, and maximum pup count during the breeding season (June–July) at the South Farallon Islands, 1977–97. Reproductive rate was defined as the maximum pup count divided by the maximum count of adult females per year. Adult sex ratio was calculated as the maximum number of adult females divided by the maximum number of adult males (bulls) counted per year. Significant ($P<0.05$) trends are shown for adult sex ratio (dashed black line) and maximum pup count (bold black line).

of the year usually remained at rookeries throughout the year (Bigg, 1988). Circumstantial evidence suggests males from California migrate northward or males from Southeast Alaska move southward in winter, or both movements take place. Large numbers of males have been seen outside the breeding season off northern California (Fry, 1939), Oregon, Washington (Mate, 1973), and southern Vancouver Island (Bigg, 1988). Total numbers of Steller sea lions are also higher in the winter than in the summer off the Canadian coast (Bigg, 1988); some winter haulouts in Canada consist almost exclusively of males (Bigg, 1988). The earliest evidence for sea lion migrations was provided by the recovery of north-coast native American spearheads from several sea lions killed off southern California in the late 1800s; and in June 1870, a spearhead used by native Alaskans was found in a large male sea lion at Point Arena, California (Scammon, 1874). Seasonal northward movement has also been documented in male California sea lions, which were similarly absent from southern sites outside the breeding season but which ranged up into Washington and British Columbia during winter (Starks, 1921; Fry, 1939; reviewed by Bartholomew, 1967).

In contrast to animals on the Farallon Islands, animals of all age classes and both sexes on Año Nuevo Island were present in significant numbers only during the breeding season from 1967 to 1990 (Le Boeuf and Bonnell, 1980; Le Boeuf et al.[3]). Data from 1962 and 1963 indicated a substantial presence of Steller sea lions at Año Nuevo through the fall and winter (Orr and Poulter, 1965) and therefore the lower numbers and, more recently, near absence of all

Figure 5

Counts of sea lions at the Farallon Islands during the breeding seasons, from 1927 to 1997. Historical counts, 1927–38: total count from single census per year conducted by boat; includes North and South Farallones and adults and sub-adults only (Bonnet et al., 1938). Historical counts, 1946–70: total count from a single census conducted each year by airplane, blimp, or boat; includes North and South Farallon Islands and may include pups, subadults and adults. Steller and California sea lions were not distinguished during these surveys. Instead all sea lions north of Point Conception were considered Steller sea lions and those south of Point Conception were considered California sea lions (Bonnot and Ripley, 1948; Ripley et al., 1962; Carlisle and Aplin, 1971). Point Reyes Bird Observatory counts, 1974–97: maximum total counts during June and July from weekly censuses at South Farallon Islands only (North Farallones excluded); includes pups, immature individuals, subadults, and adults. Means or trends over years are shown for Steller counts only (solid black lines) and for counts of Steller and California sea lions combined (dashed lines).

age classes after the breeding season may be a recent phenomenon. Similarly, Steller sea lions of various sexes and age classes were present off Humboldt County, California, only from mid-April to September (Sullivan, 1980).

Diverse seasonal patterns among sites were also evident in Canada and Alaska. In Canada, animals were usually present year-round on rookeries and numbers peaked during July, whereas year-round haulouts showed no marked seasonal variation and a variety of sexes and age classes were present in winter (Bigg, 1988). Winter haulouts were occupied only in the winter and consisted of either only males or a variety of sexes and age classes (Bigg, 1988). In Alaska, many rookeries were abandoned and some haulouts were occupied only in winter; other haulouts and rookeries were occupied year-round (Kenyon and Rice, 1961; NMML[1]). Major seasonal shifts in distribution were not evident in Alaska, although winter counts were substantially lower than summer counts and there was a greater proportion of animals at haulouts than at rookeries in winter (NMML[1]). The diversity in seasonal patterns observed among sites (including rookeries and haulouts) in California and elsewhere has confounded generalizations concerning seasonal haulout patterns, although a general shift from rookeries to haulouts in winter seems to occur throughout most of the species range.

Population status of Steller sea lions in southern and central California

Decline from historical numbers Substantial declines in Steller sea lions at the Farallon Islands have been evident since the 1920s and in recent decades. Numbers declined approximately 75–80% from an average of 600–790 animals from 1927 to 1947 to an average of 150 animals (maximum count) from 1974 to 1997 (Fig. 5). This decline may be overestimated because animals on the North Farallon Islands have not been included in surveys since 1970 and because more animals are likely visible by boat or air than from island-based vantage points (Westlake et al., 1997). However, 85% to 90% of the island is visible from vantage points and therefore effects of incomplete coverage should be small. Although the decline in numbers was severe between 1938 and 1974, the rate of decline cannot be determined for this period because surveys from this period did not distinguish Steller from California sea lions (Fig. 5). These surveys assumed that all sea lions north of Point Conception were Steller sea lions and that all sea lions south of Point Conception were California sea lions (Carlisle and Aplin, 1971). Assessing the status of Steller sea lions from the 1946–70 CDFG counts has been confounded by growth in the California sea lion population

over the same period. For example, California sea lions made up only 20% of the total sea lion count at the Farallon Islands in 1938 (Bonnot and Ripley, 1948); but by the mid 1970s, California sea lions were twice as numerous as Steller sea lions during June and July (Fig. 5).

The role of commercial harvest and direct take or harassment of sea lions by humans in this decline is uncertain. Large numbers of sea lions were hunted in California in the late 1800s for oil, hides, and "trimmings" (which included the whiskers, genitalia, and gall bladder of adult males) that were sold to Chinese markets (Scammon, 1874). Hunting sea lions for oil became unprofitable around 1900 because of the reduction in sea lion numbers and the wide-spread availability of petroleum products (Rowley, 1929). A reduced sea lion harvest for hides, trimmings, and (in Mexican waters) pet food, continued until the end of the 1930s when Chinese markets disappeared with the onset of the Japanese-Chinese war and protests were successful in stopping Mexican harvests (Bonnot, 1951). During the same period, although fewer sea lions were taken by sportsman, fisherman, and collectors for museums and zoos, rookery abandonments and population declines still persisted in Oregon and southern California (Rowley, 1929; Bonnot, 1931). An additional cause for these population declines may have been the sea lion hunts that were introduced by commercial fisheries around 1900 to reduce competition for fish (Bonnot, 1937). For example, a bounty was offered for Steller sea lions in the early 1900s in areas north of California (Rowley, 1929; Bonnot, 1931; Bonnot, 1951).

Although numbers harvested in California are not well documented and the role of harvest in the decline is not obvious, several arguments can be made that declines in Steller sea lions from the 1940s to 1970s were likely not due to effects of harvest alone. During the period of commercial harvest, Steller numbers appeared stable (Bonnot and Ripley, 1948), whereas the 75–80% decline was evident after 1947, after commercial hunting and collections had ended, although harassment by fisherman continued. After 1947, the California sea lion population increased exponentially throughout the state from 3050 in 1947 to a minimum of 18,047 in 1970 (Bonnot and Ripley, 1948; Carlisle and Aplin, 1971), whereas numbers of Steller sea lions on the Channel Islands and at the Farallon Islands declined from 80% to 100% during this period. Large increases in California sea lions were evident after commercial harvesting ended, even though many more California than Steller sea lions were likely hunted commercially, poached, or captured because of difficulty hunting in the steep, rocky intertidal areas frequented by Steller sea lions (Rowley, 1929; Bonnot, 1951). This reasoning suggests that factors in addition to harvest have influenced the population decline. Proposed causes include reduction of the prey base due to overexploitation by commercial fisheries (Ainley and Lewis, 1974), shifts in prey composition due to ocean warming, and competition for food with growing numbers of California sea lions (Bartholomew, 1967).

Human disturbance, however, likely played some role in the decline, in respect of which Steller sea lions may be more affected by human disturbance than California sea lions. For example, the large Steller sea lion rookeries at San Miguel Island and at Seal Rocks, just off San Francisco, were abandoned permanently because of harassment and shooting by hunters for sea lion trimmings or by fisherman (Rowley, 1929). Southeast Farallon Island was inhabited by fair numbers of lighthouse keepers and their families (since the mid-1800s) and egg hunters (men collecting seabird eggs for sale in commercial markets for human consumption) from the mid-1800s to the mid-1900s. Highest human occupancy occurred during World War II, when over 50 military personnel were added to the island's population (Ainley and Lewis, 1974). Families were removed in 1965 and the lighthouse was automated in 1972, after which time only PRBO researchers remained on the island (Ainley and Lewis, 1974). Despite the designation of the North and Middle Farallon Islands in 1909 and the South Farallon Islands in 1969 as a national wildlife refuge, harassment by fisherman and disturbance from low-flying helicopters was common into the 1970s (Ainley and Lewis, 1974). Heightened human presence in the mid-1900s likely increased the abandonment of Steller sea lions from the islands during the period of dramatic decline.

Recent population trends Over the last 20 years, the numbers of Steller sea lions on the South Farallon Islands has continued to decline significantly. Numbers of adult females present during the breeding season declined by 5.9% per year from 1977 to 1996, although the rate of decline has lessened since the mid to late 1980s (Fig. 3B). This rate of decline is much higher than the 3.6% per year decline reported for adult females by Sydeman and Allen (1999), who used maximum counts and data from all seasons, although rates are similar between the two studies when similar data were used (3.2% per year estimated from our study, when data from all seasons were pooled). These findings demonstrate the importance of accounting for seasonal effects when investigating population trends. The rate of decline of 5.9% per year is similar to the rate of decline observed during the breeding season in the area of greatest decline in Alaska (from Kiska Island to the Kenai Peninsula), where rates of decline varied from approximately 5% (1975–85 and 1990–94) to 16% (1985–90; York et al., 1996).

Numbers of immature individuals present during the breeding season have also declined by 4.5% per year over the past several decades, but an overall net increase in immature individuals on the islands has been apparent owing to increased numbers in the late fall and early winter. Numbers of immature individuals on the Farallon Islands in the winter were particularly high from 1984 to 1986. Immature individuals have continued to be present in significant numbers during winter in recent years. It is uncertain where these young animals originated from, but overall declines in juvenile counts, coupled with significant declines in juvenile counts during the breeding season, suggest that increased numbers in winter may represent changes in movement and haulout patterns of juveniles rather than improved juvenile survival in recent years. Increased numbers of subadult males hauled out on the South Farallon Islands during the breeding season in

recent years may have resulted from increased emigration or movement of subadult males from Año Nuevo Island due to increased competition for the declining number of females there. A stable number of adult males, coupled with declines in numbers of adult females, has resulted in a significant reduction in the adult male-to-female ratio on the South Farallon Islands during the breeding season in recent years.

These results demonstrate that reduced numbers of Steller sea lions on the Farallon Islands in recent years have been driven by reduced numbers of adult females during the breeding season, although reproductive rate and pup mortality rate were stable at this peripheral rookery. Patterns were similar at Año Nuevo, where there were sharp declines in numbers of females and pups during the breeding season but where no trend in reproductive rate was apparent from 1962 to 1990 (Le Boeuf et al.[3]). However, unlike the Farallon Islands, number of males at Año Nuevo during the breeding season also declined sharply during the same time period (Le Boeuf et al.[3]). Although the rate of decline at the Farallon Islands has lessened in recent years, large declines of 9.9% per year for pups and 31.5% per year for older animals may have occurred at Año Nuevo from 1990 to 1993, when negative effects of the 1992 El Niño may have affected estimates from this short time series (Westlake et al., 1997).

It is unknown whether reduced numbers of adult females and immature individuals present during the breeding season have resulted from reduced survival or changes in geographic distribution. Because significant declines in Steller sea lions from historical numbers and over the past several decades have occurred at San Miguel Island, Año Nuevo Island, and the South Farallon Islands, greater monitoring and protection by state or federal agencies of the southern populations are warranted. Estimates of age-class specific survival rates of females are needed to determine if reduced numbers of females are due to increased juvenile or adult mortality. More intensive studies tracking individual Steller sea lions in California are required to determine if declining numbers indicate a northward shift in the breeding range and to document migratory movements of males and females. Population dynamics and movements of prey of Steller sea lions, dietary overlap with California sea lions, and interactions of sea lions with commercial fisheries in California must be examined to determine natural and anthropogenic causes for changes in sea lion numbers or distribution.

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