Abundance and distribution of the eastern North Pacific Steller sea lion (Eumetopias jubatus) population

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Abstract—The eastern Steller sea lion (*Eumetopias jubatus*) population comprises animals that breed along the west coast of North America between California and southeastern Alaska. There are currently 13 major rookeries (>50 pups): five in southeastern Alaska, three in British Columbia, two in Oregon, and three in California. Overall abundance has increased at an average annual rate of 3.1% since the 1970s. These increases can largely be attributed to population recovery from predator-control kills and commercial harvests, and abundance is now probably as high as it has been in the last century. The number of rookeries has remained fairly constant (*n*=11 to 13) over the past 80 years, but there has been a northward shift in distribution of both rookeries and numbers of animals. Based on the number of pups counted in a population-wide survey in 2002, total pup production was estimated to be about 11,000 (82% in southeastern Alaska and British Columbia), representing a total population size as approximately 46,000–58,000 animals.

Abundance and distribution of the eastern North Pacific Steller sea lion (*Eumetopias jubatus*) population

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The Steller sea lion (*Eumetopias jubatus*) is the largest of the Otariidae and inhabits the North Pacific Rim from California to Japan. Individuals breeding at rookeries[1] located along the west coast of North America from California northward through southeastern Alaska (Fig. 1) to 144°W longitude form a distinct population segment, generally referred to as the eastern population. Historically, exchange of reproductive females with the Steller sea lion population to the north and west of 144°W longitude has been extremely low as shown by genetic studies (Bickham et al., 1996) and resightings of marked animals (Raum-Suryan et al., 2002). This indicates that population changes have been driven by birth and death rates within each population because immigration and emigration of breeding females among populations were too infrequent to affect population dynamics. More recent genetic analyses have confirmed the ancient divergence of the eastern and western populations. However, two new rookeries (White Sisters and Graves Rocks, Fig. 1) at the northern end of the range of the eastern population appear to have been colonized by females from both populations (O'Corry-Crowe et al., 2005). The number of western female immigrants to the eastern population has been small (in the 100s) to date, has not had a major impact on the growth dynamics of the overall eastern population and has been limited to the extreme northern range of the eastern population. However, the presence of breeding female immigrants from the western population within the range of the eastern population indicates that our prior assumption that population dynamics of the eastern population was completely driven by internal rates of reproduction and survival was incorrect for the past several years.

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[1] For purposes of this paper, rookeries are arbitrarily defined as traditional, terrestrial sites where >50 pups are born annually. Other terrestrial sites used by sea lions are referred to as haulouts. Small numbers of pups are also born on haulouts, but probably constitute <1% of the total <100 in the eastern population.

In recent years, attention has focused on the western Alaskan population because of a precipitous decline since the 1970s (Loughlin et al., 1992; Trites and Larkin; 1996) resulting in an "endangered" classification under the U.S. Endangered Species Act. The eastern population is currently classified as "threatened." Abundance from southern Oregon through southeastern Alaska has generally shown an increasing trend (Calkins et al., 1999; Brown et al.[2]; DFO, 2003), whereas numbers in southcentral California have declined substantially (Le Boeuf et al.[3]; Hastings and Sydeman, 2002). This is the first detailed population-wide status evaluation of abundance, trend, and distribution with a historical perspective for the eastern population. We also present the results of the first population-wide census of pup production conducted in 2002 and apply life-table analysis to estimate total population size.

In our study, we reviewed records of Steller sea lion abundance, with particular emphasis on data collected at rookeries. Some counts date back to the early 1900s, but early surveys were not systematic and methods lacked standardization, and some of the counts may have been affected by culling and hunting activities. Although these earlier survey methods preclude formal statistical analyses, the historical data provide a general sense of gross changes in abundance and distribution. Systematic surveys began in most regions along the west coast in the 1970s, but counting techniques varied among the researchers and agencies conducting the surveys, and surveys were not coordinated between jurisdictions. Nevertheless, these time series indicate changes in relative abundance within each geopolitical region. In recent years, there has been an effort to compare and calibrate counting techniques, especially for pups (Snyder et al., 2001; P. F. Olesiuk, unpubl. data), and to synthesize survey results (Loughlin et al., 1992).

Materials and methods

Count data used to estimate population trends between the late 1970s and 2004 were of two types: 1) counts of pups obtained between late June and early July (at the end of the pupping season) when most pups are <1 month of age, and 2) counts of juveniles and adults ≥1 year of
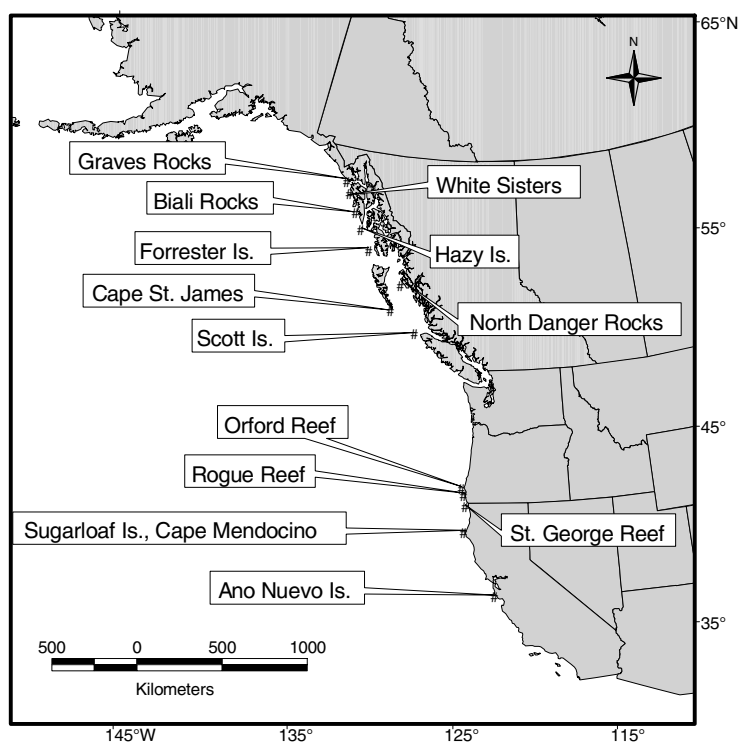

Figure 1

Geographic range of the eastern Steller sea lion (*Eumetopias jubatus*) population showing locations of major (>50 pups born) breeding rookeries.

age (i.e., nonpups) obtained from mid June to early July (mid to late in the breeding season). Steller sea lions normally give birth between late May and early July and breed between late May and mid July, although timing of these events varies somewhat geographically (Pitcher et al., 2001). Counts of pups are the preferred index to population size for many species of pinnipeds (Berkson and DeMaster, 1985). For the Steller sea lion, the vast majority of births occur at traditional rookeries, and because pups are confined to land for the first month of life, surveys of rookeries at the end of the pupping season provide a nearly complete estimate of annual pup production.

Pups are more difficult to count than nonpups because of their small size and dark color. This disadvantage is especially pronounced for counts made at oblique angles from aircraft circling rookeries or from vessels adjacent to the sites. From the mid 1970s to the late 1990s, pups were usually counted by placing people on rookeries, herding nonpups into the water, and tallying the number of pups while walking through the rookery (Calkins and Pitcher, 1982). However, the methods of obtaining such counts are disruptive to sea lions (Lewis, 1987), and counts may not be possible where rookeries are protected in parks or ecological and nature reserves. More recently, vertical 126-mm format aerial photography has been shown to be as accurate and far less disruptive (Snyder et al., 2001) for counting pups. Depending on the physical size,

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[2] Brown, R. F., S. D. Riemer, and B. E. Wright. 2002. Population status and food habits of Steller sea lions in Oregon. Report from Oregon Dept. of Fish and Wildlife to Oregon State Univ. Contract F0225A-01, 17 p. Oregon Department of Fish and Wildlife, Marine Mammal Research Program, 7118 NE Vandenberg Ave., Corvallis, OR 97330.

[3] Le Boeuf, B. J., K. Ono, and J. Reiter. 1991. History of the Steller sea lion population at Año Nuevo Island, 1961–1991. NOAA Admin. Report NMFS-SWFSC LJ-91-45C, 9 p.

substrate, and topography of rookeries, high-quality oblique 35-mm photographs can sometimes provide counts of pups with an acceptable accuracy (P. F. Olesiuk, unpubl. data). In 2002, vertical 126-mm format photography was used at all rookeries within the range of the eastern population to obtain the first estimate of total pup production (pup numbers at some rookeries had been reported previously but not for all rookeries in a single year). We have included additional counts of pups made at some sites between 2003 and 2005 for trend analyses within geographic subareas. However, only counts from the complete population-wide survey in 2002 were used to estimate total population abundance in order to provide an estimate for a single point in time.

Few reliable counts of pups were available before the 1970s, but counts of non-pups on rookeries have dated back to the early 1990s. Non-pups are easier to count, and there tends to be a high degree of correlation for counts of non-pups between oblique 35-mm format and vertical 126-mm format images (Fritz and Stincomb, 2005). However, some Steller sea lions, particularly juveniles, range widely (Raum-Suryan et al., 2002); therefore counts at haulouts within a particular geographic area may not necessarily represent the number of animals supported by local rookeries, although breeding animals show a higher degree of site fidelity. The number and proportion of various sex and age classes of non-pups that are hauled out varies with season, time of day, and (in some cases) with tide (Winthrow, 1982; Calkins et al., 1999).

Counts from the 2002 population-wide survey (Table 1) indicated a fairly tight relationship between the number of pups and nonpups counted on rookeries (Fig. 2). A similar pattern was noted for rookeries in British Columbia and the relationship persisted over the three decades concurrent pup and nonpup counts were available (P. F. Olesiuk, unpubl. data). The historical counts of nonpups (or total animals where pups and nonpups were not distinguished) on rookeries thus likely provide a general index of the size of the breeding population associated with each rookery.

Systematic surveys have been conducted to monitor trends of the eastern Steller sea lion population, but methods and schedules have varied depending on the agency conducting the surveys. In southeastern Alaska, the Alaska Department of Fish and Game periodically conducted ground counts of pups on rookeries from 1979 through 1998, and used vertical 126-mm format photography to count pups since 1998. In British Columbia, the Department of Fisheries and Oceans has conducted province-wide aerial surveys of rookeries and haulout sites at 2–5 year intervals since the early 1970s, using oblique 35-mm format photography to count both pups and nonpups. In 1998 and 2002, both pups and nonpups were counted at British Columbia rookeries with the use of vertical 126-mm format photography. There are no Steller sea lion rookeries in Washington, but the Washington
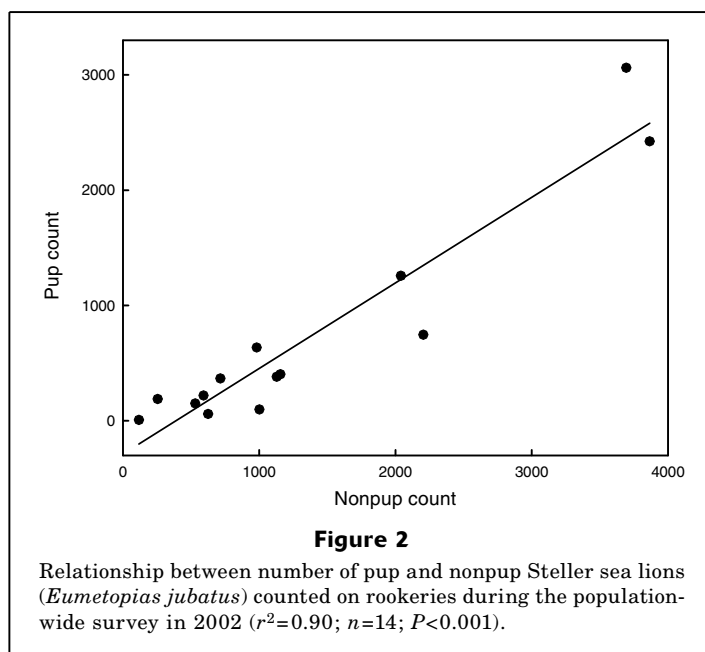
Table 1

Counts of pups and nonpups for each rookery and for all haulout sites combined by region for the population-wide survey of the eastern Steller sea lion (*Eumetopias jubatus*) population in 2002. Pup counts were made from vertical 126-mm format images, and nonpup counts from either vertical 126-mm format images or oblique 35-mm photographs. Nonpup counts included counts of pups at the indicated number of major sites (used by >50 animals on a regular basis during the breeding season), as well as counts of pups at numerous minor sites and counts of a few scattered animals.

Site	Pups	Nonpups
Southeastern Alaska		
Graves Rocks	98	1001
White Sisters	403	1156
Biali Rocks	59	625
Hazy Islands	1257	2050
Forrester Island	3060	3699
Haulout sites (20 major sites)	9	6752
Southeastern Alaska total	4886 (49%)	15,283 (43%)
British Columbia		
North Danger Rocks	207	592
Cape St. James	655	982
Scott Islands	2451	3865
Haulout sites (24 major sites)	5	6681
British Columbia total	3318 (33%)	12,120 (34%)
Washington		
Haulout sites (2 major sites)	0 (0%)	651 (2%)
Oregon		
Orford Reef	382	1178
Rogue Reef	746	1264
Haulout sites (7 major sites)	8	1727
Oregon total	1136 (11%)	4169 (12%)
California		
Saint George Reef	367	716
Sugarloaf Island-Cape Mendocino	150	588
Año Nuevo Island	189	255
Haulout sites (6 major sites)	7	1543
California total	713 (7%)	3102 (9%)
Eastern population	10,053	35,325

Department of Fish and Wildlife has conducted numerous aerial surveys of haulout sites during the breeding season using oblique 35-mm format photography since 1978. In Oregon, the Oregon Department of Fish and Wildlife has conducted state-wide aerial surveys of nonpups on rookeries and haulouts using oblique 35-mm format photography on a nearly annual basis since the mid-1970s and has periodically obtained ground, or more recently vertical 126-mm format or high-resolution digital 35-mm format, pup counts. In California, the National Marine Fisheries Service, Southwest Fisheries Science Center, conducted statewide surveys during early July beginning in 1996 using vertical 126-mm format photography to count pups and nonpups at all rookeries and haulout sites. Time series of counts that were obtained with assorted methods were also available for some rookeries in California dating back to the 1970s. Although these surveys provide reliable information on changes in relative abundance within each region or at a particular rookery, they are difficult to synthesize into a population-wide assessment because of uncoordinated survey schedules and methods. Given the consistency within, but inconsistency between, these geo-political jurisdictions, we assessed trends in abundance by region (southeastern Alaska, British Columbia, Washington, Oregon, and California). Counts for each region were converted to natural logarithms and then regressed on year to determine average annual population growth rates.

We estimated the total population size in 2002 from the predicted ratio of pups to nonpups in the population (Calkins and Pitcher, 1982; Trites and Larkin, 1996). From life tables for a stable sea lion population in the Gulf of Alaska, Calkins and Pitcher (1982) estimated total population size to be about 4.5 times the number of pups born. In order to apply this approach to the eastern population, which was not stable but increasing (see "Results" section), we conducted sensitivity analyses to determine how this multiplier varies with population growth rate (λ) by incrementally changing each of the life history parameters that affect it, namely juvenile mortality rates, adult mortality rates, age at maturation, and fecundity rates (Lotka, 1907; Cole, 1954) .

We also reviewed historical records of Steller sea lion abundance in an attempt to relate current population size with abundance prior to the initiation of standardized surveys. Although these records provide insights into relative population levels, caution must be used because the older counts were obtained by a variety of methods and the seasonal timing of counts was inconsistent. In most cases the counts were made by professional biologists or naturalists hired by government agencies to conduct sea lion investigations, and special trips were made to rookeries to obtain first-hand counts; therefore it is unlikely numbers were grossly in-

Figure 2

Relationship between number of pup and nonpup Steller sea lions (*Eumetopias jubatus*) counted on rookeries during the population-wide survey in 2002 ($r^2=0.90$; $n=14$; $P<0.001$).

accurate. Because of the *ad hoc* nature of these counts, it was difficult to synthesize them into even a regional estimate of abundance, or to conduct statistical analyses; therefore these counts were generally examined on a rookery-by-rookery basis (Appendix).

Results

Southeastern Alaska

Counts of Steller sea lion pups in southeastern Alaska increased from 2219 in 1979 to 5510 in 2005 (Fig. 3A), representing an average annual rate of increase of 3.2% ($r^2=0.91$; $n=10$; $P<0.001$). Prior to the early 1980s, the only rookery in southeastern Alaska was the Forrester Island complex. Only 50–100 animals were recorded when the site was first noted in the 1920s, and 350 animals were recorded when the site was revisited in 1945, and there was no mention of pupping in either case (Rowley, 1929; Imler and Sarber, 1947). Thus, although count data are extremely limited, it appears that Steller sea lion abundance was probably quite low in southeastern Alaska during the first half of the 20th century. Counts are not available, but the Forrester Island rookery must have grown dramatically through the 1950s and 1960s (Fig. 4A). By the time the first aerial survey was conducted in 1961, Forrester Island had grown to about one-third its current size in terms of both the numbers of pups and nonpups (Bigg, 1985). However, increases at Forrester Island appear to have slowed since the late 1970s, showing only a slight increase in pup production (0.6% per year; $r^2=0.40$; $n=13$; $P=0.021$) and no discernible increase in the number of nonpups ($r^2=0.22$; $n=12$; $P=0.125$).

With the slowing of growth on Forrester Island, several new rookeries were established in southeastern Alaska (Calkins et al., 1999) (Appendix I). Hazy Islands were a substantial haulout in the 1950s (Mathisen and Lopp, 1963), but pup counts increased after they were first observed in 1979 (13% per year, $r^2=0.76$; $n=11$; $P<0.001$). White Sisters developed into a rookery in the early 1990s and counts of pups also increased rapidly (16% per year, $r^2=0.87$; $n=10$; $P<0.001$). In recent years, Graves Rocks and Biali Rocks appear to be developing into rookeries; 175 and 100 pups were counted respec-

tively at the two sites in 2005. Growth of these four new rookeries accounted for about 48% of the increase in total pup production in southeastern Alaska during the 1980s, and for about 74% of the total increase since 1990.

In addition to the five rookeries, sea lions use about 20 major haulout sites (>50 animals) and several smaller sites in southeastern Alaska on a regular basis during the breeding season, as well as numerous other sites during the nonbreeding season. During the 2002 survey, a total of 6752 nonpups were counted at haulout sites and another 8531 nonpups were counted at rookeries (Table 1).

British Columbia

There are currently three Steller sea lion rookeries in British Columbia: the Scott Island complex (Triangle, Beresford-Maggot, and Sartine Islands), Cape St. James, and North Danger Rocks. Counts of pups from oblique 35-mm format photographs increased from 941 in 1971 to 3276 in 2002 (Fig. 3B), representing an average annual rate of increase of 3.2% ($r^2=0.71$; $n=9$; $P=0.005$), similar to the overall rate observed in southeastern Alaska. However, piecewise regressions provide a better fit to the time series of pup counts, indicating that most of this increase has occurred since the 1980's ($r^2=0.85$; $n=9$; $P=0.002$). Significant increases in pup production ($P<0.005$) were evident at all three rookeries (Appendix), but mean rates varied among sites (3.7% at Scott Islands, 2.0% at Cape St. James, and 2.7% on North Danger Rocks). Numbers of nonpups on rookeries also increased significantly ($r^2=0.89$; $n=9$; $P<0.001$), paralleling the increases in pup production (Fig. 3B).

Counts on rookeries in British Columbia date back to 1913 (Newcombe and Newcombe, 1914) and indicate breeding populations were historically large (Fig. 4B). Extensive sea lion reduction programs were conducted in British Columbia from 1912 through 1966, and attempts were made to commercially harvest sea lions during the 1960s. One major rookery, the Sea Otter Group, was eradicated by intensive control efforts during the 1920s and 1930s. The site was visited each year toward the end of the pupping season and all pups and as many nonpups as possible were killed, and by about 1940 it was no longer used as a rookery. Predator-control kills and commercial harvests in British Columbia continued into the 1960s and impacted all rookeries, and the breeding population was reduced to about 30% of peak levels by the late 1960s (Bigg, 1985). It appears that numbers at Scott Islands have fully recovered from these kills, but numbers at the two other rookeries are still below historical peak levels (Appendix).

Sea lions also currently use 24 major haulout sites (>50 animals) in British Columbia on a regular basis during the breeding season, up from 18 sites when systematic province-wide surveys were initiated in the early 1970s (Bigg, 1985). Numbers of animals counted on these sites increased at rate of 4.0% since the early 1970s ($r^2=0.82$; $n=9$; $P<0.001$), which is not significantly different from
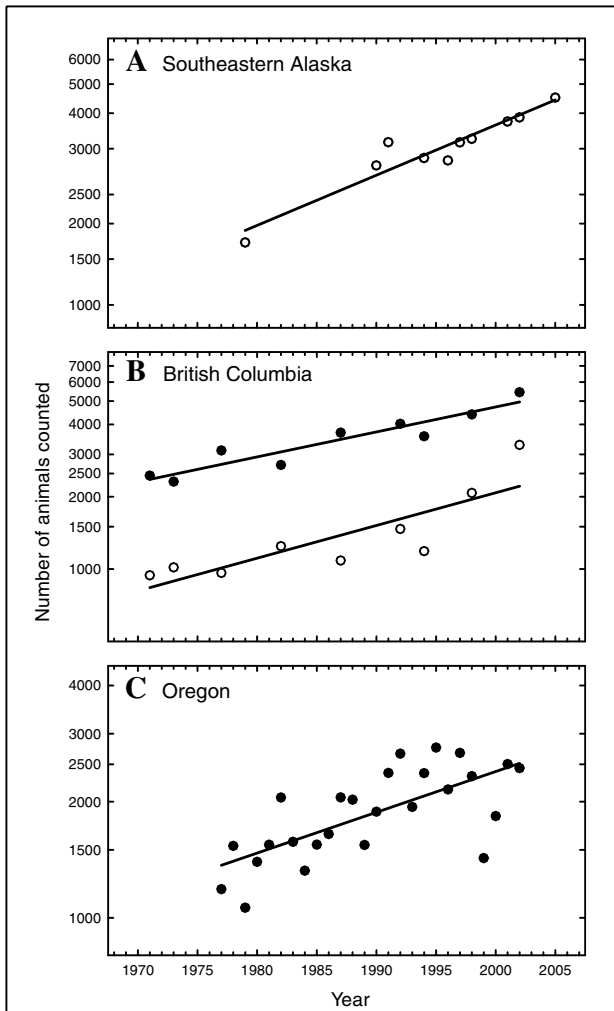

Figure 3

Recent trends in counts of Steller sea lion (*Eumetopias jubatus*) pups (○) and nonpups (●) on rookeries in (**A**) Southeastern Alaska, (**B**) British Columbia, and (**C**) Oregon. These areas combined account for over 90% of pup production in the eastern population. Survey techniques were standardized within each region, but differed among regions. The slopes are all statistically significant ($P<0.001$), and none differed significantly from the overall rate of increase of 3.1%.

the rate of growth observed on rookeries. During the 2002 survey, 6681 nonpups were counted on haulout sites, and another 5439 on rookeries (Table 1).

Washington

There are no rookeries in Washington, but Steller sea lions are found along the coast throughout the year. Four haulouts, including two major sites (>50 animals), are regularly used during the breeding season. Since 1989, surveys have been conducted almost annually, and numbers of sea lions counted have increased at an average annual rate of 9.2% (r^2=0.38; n=37; P<0.001). These animals are assumed to be immature animals and nonbreeding adults associated with rookeries from other areas. Juvenile sea lions branded as pups on Forrester Island in southeastern Alaska (Raum-Suryan et al., 2002) and on Rogue Reef in Oregon (R. F. Brown, unpubl. data) have been observed in Washington.

Older records indicate that current abundance on the Washington coast is reduced from historical levels (Fig. 4C). Between 2000 and 3000 Steller sea lions were reported to be present during August and September of 1914, 1915, and 1916 on Jagged Island (Kenyon and Scheffer, 1959), compared with a maximum statewide breeding season count of 847 during 1978–2001. Washington State Department of Fisheries offered a bounty of $8.00 for sea lions between 1944–48, but in 1949 this was reduced to $3.00 and limited to inside waters because aerial patrols indicated that the main coastal haulouts at Jagged Island and Split Rock had been reduced from 600 sea lions in the 1930s to fewer than 100 by 1949 (Scheffer, 1950). Only sporadic counts were available for individual sites during the 1950s and 1960s, but they indicate that few sea lions (<100 animals) were present during the breeding season and that total abundance did not exceed 500 during any season by the 1950s (Scheffer, 1950; Kenyon and Scheffer, 1959).

Oregon

Steller sea lions breed and pup at two rookeries, located at Rogue Reef and Orford Reef, and occupy seven major haulout sites in Oregon during the breeding season. The total number of nonpup sea lions on rookeries increased from 1186 in 1977 to 2442 in 2002 (Fig. 3C), representing an average annual rate of increase of 2.5% (r^2=0.49; n=26; P<0.001). Although not as well documented, pup numbers also appear to have increased. In 1990, 492 and 298 pups were observed during ground counts at Rouge Reef and Orford Reef respectively, compared with 746 and 382 pups on 126 mm format images in 2002 (2.3% average annual rate of increase). During the 2002 population-wide survey, an additional 1727 nonpups were counted at haulout sites in Oregon (Table 2).

Historical data on Steller sea lion abundance in Oregon are few (Fig. 4D). Pearson and Verts (1970) counted 862 animals (including some pups) during a state-wide aerial
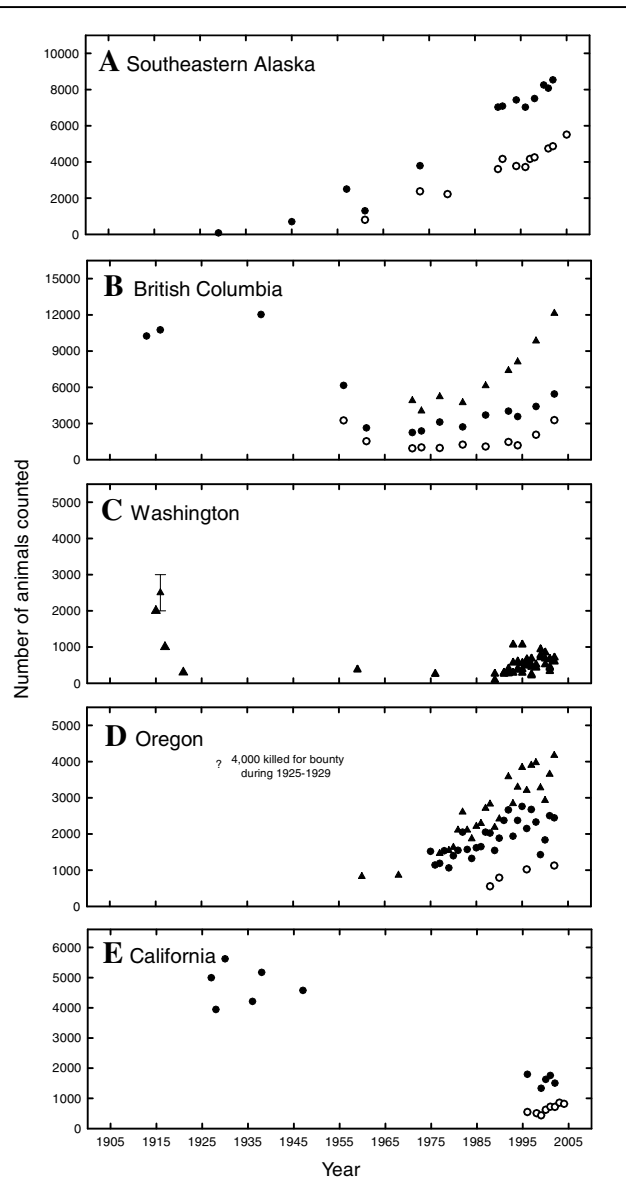

Figure 4

Historical counts over the last century of Steller sea lion (*Eumetopias jubatus*) pups (○), non-pups on rookeries (●), and total nonpups on rookeries and haulouts (▲) for (**A**) Southeastern Alaska, (**B**) British Columbia, (**C**) Washington, (**D**) Oregon, and (**E**) California.

survey in June 1968, somewhat lower than the 1977 nonpup count of 1461 animals. The largest rookery was Orford Reef, where 475 animals, including pups, were counted. Interestingly, only 125 animals were reported at Rogue Reef, which is currently the largest rookery in Oregon, and Pearson and Verts (1970) suggested that it was no longer used as a rookery. Earlier counts are lacking, but the population was presumably substantially larger in the 1920s because about 4000 sea lions were

Table 2

Results of life-table sensitivity analyses showing the potential change in ratio of total population size to pups for a population increasing at 3.1% per annum. The vital rates in Calkins and Pitcher's (1982) life tables[1] for a stable population of Steller sea lions (*Eumetopias jubatus*) were incrementally adjusted until a population growth rate, λ, of 3.1% was attained. The corresponding stable sex- and age-distributions were calculated by using Cole's (1954) finite approximations of Lotka's (1907) population equations.

Parameter that changed	Relative change	Population growth rate (λ)	Pup multiplier
Δ Mortality all ages	−15%	3.1%	5.0
Δ Juvenile mortality	−27%	3.1%	5.2
Δ Adult mortality	−33%	3.1%	4.7
Δ Fecundity	+32%	3.1%	4.2
Δ Age at maturation	−1.6 years	3.1%	4.2

[1] Calkins, D. G., and K. W. Pitcher.   1982.   Population assessment, ecology and trophic relationships of Steller sea lions in the Gulf of Alaska.   *In* Environmental assessment of the Alaskan continental shelf. p. 447–546.   U.S. Department of Commerce and U.S. Department of Interior, Final Report of Principal Investigators 19:1–565.

killed for bounty on the Oregon coast during 1925–29 (Pearson and Verts, 1970), although some of these may have been nonbreeding animals associated with rookeries in California, British Columbia, and Alaska.

California

Steller sea lions historically have used six rookeries in California (San Miguel Island, Año Nuevo Island, the Farallon Islands, Seal Rocks off San Francisco, Sugarloaf Island-Cape Mendocino, and Saint George Reef). San Miguel Island and Seal Rocks are no longer used by Steller sea lions and only a few pups have been born on the Farallon Islands each year since the 1980s. There may have also been several additional small rookeries south of Año Nuevo (Bonnot, 1928; Rowley, 1929).

Statewide surveys, with the use of vertical 126-mm format aerial photography, were implemented in California in 1996. From 1996 through 2004 there was no discernible statewide trend for nonpups on rookeries (r^2=0.408; n=7; P=0.123), however, pup production increased at an average annual rate of 8% (r^2=0.68; n=8; P=0.012).

Although there has been a long and intermittent time series of counts for rookeries in California over the last 75 years (Bonnot, 1928, 1929; Bonnot and Ripley, 1948; Bartholomew and Boolootian, 1960; Orr and Poulter, 1967; LeBoeuf et al., 1991; Stewart et al., 1993), caution is warranted when attempting to evaluate population trends from the older data because they are drawn from a variety of sources where different survey methods were used. Statewide, total counts of nonpups at the six rookeries during the first half of the 20th century were on the order of 3900–5600. The 2004 count at these same six sites was 1578 nonpups and 818 pups—indicating that, perhaps, only about a third as many animals are currently present in the state (Fig. 4E). Population trends differed markedly among sites (Appendix).

Historically, Steller sea lions extended south to the Channel Islands in southern California, and San Miguel Island was considered to have been the southernmost

rookery (Bonnot, 1928, 1929). It appears that Steller sea lion were once more abundant than California sea lions (*Zalophus californianus*) in that area (Bartholomew, 1967). Steller sea lions were reported to breed there in small numbers; Bonnot (1929) counted 50 pups in 1928. Abundance of nonpups in the Channel Islands peaked at about 2000 in the late 1930s (Appendix), although hunting and harassment could have resulted in fewer animals being present during the surveys (Bonnot and Ripley, 1948; Stewart et al., 1993). Numbers subsequently declined—the main declines occurring between the late 1930s and 1950s (Bartholomew and Boolootian, 1960; Bartholomew, 1967). No births have been recorded since 1982 and no adults have been seen since 1983 (Stewart et al., 1993).

In central California, Steller sea lion abundance at Año Nuevo and the Farallon Islands is currently only about 20% of the levels reported between the 1920s and 1960s (Appendix). Steller sea lions had deserted the rookery at Seal Rocks near the entrance to San Francisco Bay by the late 1920s, purportedly as a result of persistent harassment by fishermen (Rowley, 1929). During the 1920s, Año Nuevo Island and the Farallon Islands were identified as the most important rookeries in California, with 625 and 400 pups counted at each site, respectively, in 1922 (Bonnot, 1929). On Año Nuevo, numbers remained at high levels until the early 1960s, then declined thru the mid-1990s (Orr and Poulter, 1967; Le Boeuf et al., 1991) (Appendix). Since 1996, both pup production (r^2=0.035; n=8; P=0.656), and nonpup numbers (r^2=0.018; n=8, P=0.755) have been stable. Fewer counts are available for the Farallon Islands, but the pattern appears to be similar (Appendix); abundance was at high levels from the 1920s to early 1960s and then declined sharply during the 1960s or early 1970s (Hastings and Sydeman, 2002). Pup production on the Farallons has been low since at least 1974 (Appendix). An average of only nine pups was counted between 1996 and 2004 and the site presently does not meet our criteria for a rookery (>50 pups). Nonpup numbers were stable (r^2=0.173;
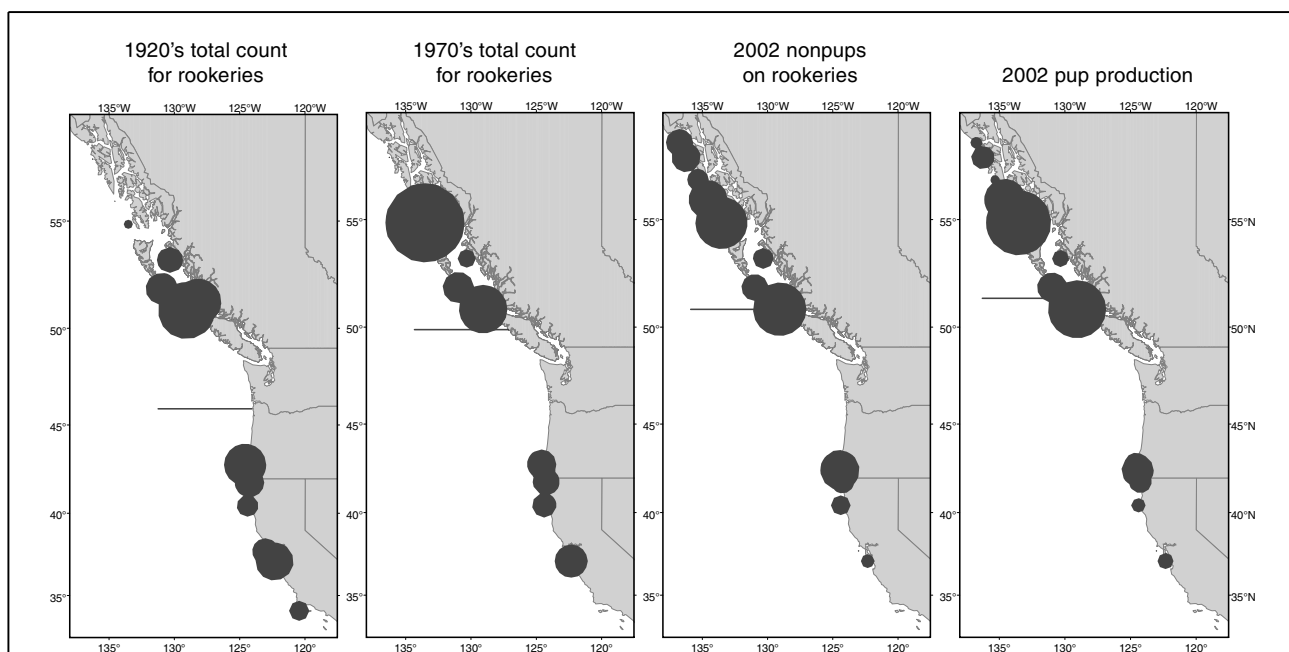
Figure 5

Map showing the shift in distribution and relative importance of rookeries in the eastern Steller sea lion (*Eumetopias jubatus*) population. Circles represent the proportion associated with each rookery of the total estimated abundance in the 1920s (1913–17 for British Columbia) and 1970s; and the proportion of nonpups and pups associated with each rookery during the 2002 range-wide survey. The horizontal lines indicate the center of the distribution (the latitude of each rookery weighted by the number of animals on it). For the 1920s, rookery counts in California represent minimum abundance because pups were not always included. Historic counts were unavailable for Oregon; therefore the minimum abundance was taken as the number killed for bounty during 1925–29. Because Oregon lies near the estimated center of the breeding distribution, the center of distribution is insensitive to the numbers assumed on Oregon rookeries (halving or doubling the Oregon figures shifts the center by less than 0.5° of latitude).

$n=15$; $P=0.123$) at low levels (Appendix) between 1974 and 2004.

Steller sea lions have been counted only sporadically at the Sugarloaf-Cape Mendocino and Saint George Reef rookeries in northern California until recent years (Appendix). Numbers of nonpups have been relatively stable since 1996 at both Sugarloaf-Cape Mendocino ($r^2=0.106$; $n=8$; $P=0.431$) and Saint George Reef ($r^2=0.128$; $n=9$; $P=0.345$). A comparison of counts made during the 1927–47 period with recent counts (Appendix) indicates that current abundance is probably only slightly reduced from historical levels. The Sugarloaf-Cape Mendocino rookery is small; counts of pups increased from 62 in 1996 to 131 in 2004, representing an average annual increase of 13% ($r^2=0.725$; $n=8$; $P=0.007$). For the Saint George Reef rookery, located near the California-Oregon border, counts of pups increased from 243 in 1996 to 444 in 2004, representing an average annual rate of 10% ($r^2=0.70$; $n=8$; $P=0.009$). Over the same period, counts of nonpups showed no discernible trend ($r^2=0.11$; $n=12$; $P=0.431$).

Steller sea lions use about six major (>50 animals) haulout sites along the California coast between Saint George Reef and Año Nuevo Island, as well as numer-ous smaller sites, during the breeding season. In 2002, a total of 1543 nonpups were counted at haulouts, in addition to the 1559 nonpups counted on rookeries. At least 12 former Steller sea lion haulout sites and perhaps a few rookeries between the Channel Islands and Año Nuevo Island (Bartholomew and Boolootian, 1960; Bonnot, 1928; Bonnot and Ripley, 1948; Rowley, 1929) have been abandoned.

Overall trend for the eastern North Pacific Steller sea lion population

The eastern North Pacific Steller sea lion population has exhibited significant and similar annual rates of growth in all three regions that support the largest rookeries: 3.2% in southeastern Alaska, 3.2% in British Columbia, and 2.5% in Oregon (Fig. 3). Combining the trend trajectories for these three regions, which currently account for over 90% of total pup production in the eastern population, overall abundance is estimated to have increased by about 215% over the last 25 years, representing an annual rate of increase of 3.1%. The time series for California is shorter; however pup production increased significantly at 7% per year between 1996 and 2004.

With the exception of the southernmost rookery at Año Nuevo Island and the (former) Farallon Islands rookery, both greatly reduced from historical levels, pup production has increased consistently throughout the range of the eastern population over the past 25+ years.

The total population-wide pup count in 2002 was 10,053 pups, of which 49% were found in southeastern Alaska, 33% in British Columbia, 11% in Oregon, and 7% in California (Table 1). This represents minimum pup production because some pups may have died and disappeared from rookeries prior to the survey, or were born after the census. Following Trites and Larkin (1996), we applied an arbitrary adjustment of 10% to account for pups that had been missed during our survey, giving a pup production estimate of 11,060. Using life tables, Calkins and Pitcher (1982) estimated the ratio of total animals to pups in a stationary population would be about 4.5:1. Our sensitivity analyses indicated that for a population increasing at 3.1%, the ratio could be as low as 4.2:1 if the growth were due to increased fecundity, or as high as 5.2:1 if the growth was due to reduced juvenile mortality (Table 2). The eastern population is thus estimated to have numbered about 46,000–58,000 animals in 2002. During the 2002 survey, we actually counted 45,378 animals (10,053 pups and 35,325 nonpups) on rookeries and at haulouts. This count represents an absolute minimum population size because not every site was surveyed and some animals were absent from rookeries and haulouts during the surveys and therefore were not counted.

The general sparseness and lack of standardization of the pre-1970 counts prevents a rigorous comparison of current and historical population levels; however several clear patterns emerge (Appendix). In southeastern Alaska abundance was apparently quite low during the first half of the 20th century, but numbers have increased consistently since that time. We have no explanation for the low numbers during the early 1900s because we are not aware of large-scale hunting or predator control efforts. Numbers were high in British Columbia in the early 1900s but were then reduced by about 70% by predator control and hunting. They have since recovered to levels approximately two-thirds of those of the early 1900s. Numbers on haulouts in Washington State were severely reduced by bounty hunting in the early to mid-1900s. Although there has been substantial recovery, peak numbers still appear to be only about half of levels of 1915. There are no count data available for Oregon prior to 1968, but the fact that about 4000 sea lions were killed for bounty during 1925–29 would indicate a sizable population at that time. There has been a substantial recovery since the 1968 surveys. The California population was apparently large during the early 1900s. Sites in southern California began declining in the late 1930s and that portion of the range was abandoned by the 1980s. Numbers in central California remained high into the 1960s, then declined to low levels, and stabilized during the 1990s. In northern California numbers were likely reduced during the mid 1900s, but now appear

to be approaching levels of the early 1900s. Overall, the eastern population currently appears to be similar in size to historical levels of the early 1900s; the large population increase in southeastern Alaska balances out the declines in the southern portion of the range.

Although the number of rookeries used by the eastern Steller sea lion population has remained relatively constant (range 10–13), their distribution has shifted (Fig. 5). In the 2002 survey, the breeding population was centered (the latitude of each rookery weighted by the number of animals on it) at about 51.5°N (central British Columbia coast). Just over half of the rookeries (7 of 13) and births (57%) occurred north of that latitude, with the northernmost rookery at 58.2°N. For the 2002 population-wide survey, the pattern was similar for both pups and total numbers (pups and nonpups), suggesting they both provided an index of breeding distribution. In comparison, during the 1970s the breeding population was centered at roughly 49.9°N (central Vancouver Island), with the northernmost rookery at 54.8°N, representing a northward shift of 0.5° of latitude or 65 km per decade. In the 1920s, the breeding population was probably centered somewhere around 46.0°N (Washington-Oregon border); only two small rookeries accounted for about 13% of total abundance situated north of 51.5°N (the current center of pupping). At the southern end of their range, the declines of Steller sea lions appear to have begun in southern California (San Miguel) between the late 1930s and 1950s, and were followed by declines in central California between 1960 and 1990; however the two northernmost sites in California exhibited relative stability. Conversely, at the northern end of their range, Steller sea lions probably began breeding in significant numbers in southern southeastern Alaska (Forrester Island) in the late 1940s or 1950s and extended their breeding range to central southeastern Alaska (Hazy Islands) in the early 1980s, and northern southeastern Alaska (White Sisters) in the 1990s. Overall, the southern end of the breeding range contracted by about 3° latitude (330 km), and the northern limit was extended by about 5° latitude (550 km).

Discussion

The population increases observed in recent years over most of the range of eastern North Pacific Steller sea lion population almost certainly represent recovery from the impacts of prior predator-control programs, harvesting, and indiscriminate killing that took place prior to protection under the Canadian Fisheries Act of 1970 and implementation of the U.S. Marine Mammal Protection Act in 1972. The overall annual rate of increase of 3.1% was widespread (from Oregon to southeastern Alaska) and has been underway for at least 25 years, and there is no evidence of it slowing with increasing sea lion densities. The consistent, long-term observed rate of increase of 3.1% throughout most of the range of the eastern population is well below the theoretical maximum intrinsic rate of increase for pinnipeds

(Wade, 1998; Harkonen et al., 2002). This annual rate of increase indicates that either some factor or factors are still limiting the growth rate of this population or that the growth potential of this otariid is less than the theoretical maximum, which was derived from phocid population growth rates. We have observed Steller sea lions that have been shot or entangled in marine debris, and this undocumented mortality could be preventing the population from increasing at a higher rate. In addition, the Steller sea lion tends to have a longer period of maternal investment and a lower reproductive rate than most phocids (Pitcher et al., 1998), both of which may limit the growth potential of populations.

Although the three geographic regions supporting the largest rookeries all increased at about the same rate, individual rookeries often exhibited different population growth rates or temporal changes in growth rates. At the northern end of the range, Forrester Island accounted for essentially all of the population growth until the 1970s; however the observed rate of change has slowed since the 1980s. At the same time, some of the rookeries to the south of Forrester Island in British Columbia and to the north of it in central-northern southeastern Alaska have exhibited higher-than-average growth rates since the 1980s. The mechanism causing these geographic patterns is unknown, but could involve 1) dispersal of breeding animals between rookeries, 2) differences in local conditions that affect reproduction and survival, or 3) a shift in distribution of prey resources. Some dispersal of breeding females from their natal rookeries has been shown to occur. Six of 31 females that were marked as pups on the Forrester Island rookery were subsequently observed to have given birth on other rookeries (Raum-Suryan et al., 2002). The authors of that study concluded that the Steller sea lion generally conformed to the metapopulation concept as depicted by Hanski and Simberloff (1997), in that local breeding populations (rookeries) and movements among these local populations have the potential of affecting local dynamics.

For our assessment of long-term historic population trends, we relied mainly on counts of non-pups (or occasionally pups and nonpups combined) on rookeries, as few reliable pup counts were available prior to the 1970s. The 2002 population-wide survey (Fig. 2) and the last 30 years of counts in British Columbia indicated there is a relationship between the numbers of nonpups and pups on rookeries. However, departures from this relationship can occur, especially where existing rookeries are being abandoned or new rookeries are being formed. For example, the Farallon Islands, which no longer meet our definition of a rookery, now serves largely as a haulout site (Le Boeuf et al., 1991). The historical rookery on the Sea Otter Group in British Columbia, the only rookery known to have been extirpated by control efforts, is also still used during the breeding season as a haulout by nonbreeding animals. Conversely, in southeastern Alaska, the new rookeries were established at sites previously used as major haulouts by nonbreeding animals. The lack of accurate pup counts may, thus, have influenced our historical interpretation of historical data and our

depiction of the exact breeding range, but there is a general consensus that the breeding range has shifted. Pup production in southern California has disappeared and in central California has dropped to less than one-fifth of what it was in the 1920s. Few, if any, pups were born in southeastern Alaska in the early 1900s, whereas this area now accounts for nearly half of total pup production in the eastern North Pacific population.

Control programs and harvesting clearly depleted the eastern Steller sea lion population and may have contributed to its redistribution, but the kills cannot fully explain the shift in the distribution. For example, while control efforts were underway in British Columbia during the 1950s and 1960s, animals may have taken refuge just north of the British Columbia-Alaska border at Forrester Island, or animals breeding on Forrester Island may have benefited from reduced competition as a result of the reductions on British Columbia rookeries. However, the northward expansion of the breeding range in southeastern Alaska continued through the 1980s and 1990s, even though killing of sea lions in British Columbia ceased in the 1960s. At the southern end of their range, sea lions were apparently very abundant in California before the 1860s, but were depleted during the 1870s because of intense hunts of sea lions for oil and hides (Bonnot, 1929). The last organized kills were made in 1909, although hunting, especially of bulls for trimmings (genitals, lips with whiskers, and gall bladders) continued into the 1930s. Nevertheless, the population declines in southern California began in the late 1930s, and in central California began in the late 1960s and early 1970s, well after major kills by humans had ended (Hastings and Sydeman, 2002).

The reason for the northward shift in the overall breeding distribution is unknown, and different factors may have been in play at the southern and northern ends of the range. In the south, competition with increasing populations of other pinnipeds may have been a factor in range constriction (Stewart et al., 1993). In particular, the number of California sea lions breeding in California increased from at most a few thousand in the 1920s (Bonnot, 1928) to about 240,000 in 2000 (Lowry and Maravilla-Chavez, 2005). It is likely that California sea lions and Steller sea lions compete with each other because 1) their ranges overlap, 2) they share the same haulout sites, and 3) they probably consume many of the same prey species. On San Miguel Island and the Farallon Islands, where Steller sea lions used to predominate (Bartholomew and Boolootian, 1960; Ripley et al., 1962; Stewart et al., 1993), the declines in Steller sea lions coincided with large increases in numbers of California sea lions (Stewart et al., 1993; Hasting and Sydeman, 2002).

For unknown reasons, southeastern Alaska represents the only area throughout the range of the eastern North Pacific population where new Steller sea lion rookeries have been established. Steller sea lion rookeries are normally located on remote, offshore islands or reefs and require adequate areas above high water levels where young pups can survive most weather conditions. There

must also be adequate prey on a consistent basis within the foraging range of lactating females. Perhaps the limited availability of such sites has restricted the establishment of new rookeries at other locations.

Changes in the ocean environment, particularly towards warmer water temperatures (Field et al., 2006), have also been proposed as a factor that has favored the California sea lion and other pinnipeds over the Steller sea lion in the southern part of their range (Bartholomew and Boolootian, 1960). Environmental conditions can affect sea lion populations directly or indirectly. Temperature could directly affect the survival of animals and such effects would be expected to be most evident at the latitudinal extremes of the range. The ocean environment can also act indirectly by affecting marine food webs, and thus the quantity and quality of prey available to sea lions. Unfortunately, with historical survey data being so scant, and with sea lions having been artificially reduced below natural levels, one can only speculate about the long-term effects of environmental conditions on the eastern Steller sea lion population, but conditions currently appear to be favorable through much of their range.

A somewhat similar change in Steller sea lion distribution and the establishment of new rookeries have been noted along the Asian coast. There the southern range limit has moved northward by 500–900 km over the past 50 years and several new rookeries have been established (Burkanov and Loughlin, in press).

Based on the population-wide survey in 2002, pup production for the eastern population is currently estimated to be about 11,000, and total abundance on the order of 46,000–58,000. It should be emphasized that this should be regarded as a "general" estimate because several factors can affect the accuracy of pup counts and correction factors. Following Trites and Larkin (1996), we added 10% to pup counts to estimate pup production (i.e., actual number of births), which seems reasonable, but the adjustment is subjective and arbitrary, and in reality the adjustment probably varies from site-to-site and year-to-year. The sex and age structure of populations, and hence the ratio of pups to nonpups, may differ between populations and change with population status in ways we do not understand. We attempted to delineate the possible range of changes in the correction factors by using sensitivity analyses, which showed the multiplier could either decrease if population productivity is controlled by fecundity or age at maturation, or increase if population productivity is controlled by mortality. Assessments for the western North Pacific population have indicate that the population declines were primarily due to poor juvenile survival (York, 1994), and if this is in fact the main determinant of population growth, the pup multiplier and estimated abundance of the eastern population may lie toward the high end of our range.

During the 2002 population-wide survey, a surprisingly large number of nonpups were observed (75–100% of the number expected based on our life table analysis). Because one would expect appreciable numbers of juveniles and adults to be dispersed at sea and missed during surveys, the actual size of the eastern population

may be near the upper end of our estimated range. On the other hand, 2002 may merely have been an exceptional year for pup production, although the more recent pup counts available for California (2003 and 2004) and southeastern Alaska (2005) indicate that pup numbers have continued to increase. The apparent surplus of nonpups observed during the 2002 survey could also be indicative of the presence of nonbreeding animals associated with the western population in our survey area. Studies (where sea lions have been branded) have shown there is some overlap in the nonbreeding range of the two populations (Raum-Suryan et al., 2002), although there is no reason to expect a higher degree of movement from west to east. Moreover, the observed ratios of total counts to pup counts was uniformly high over the entire range of the eastern population (4.1 in southeastern Alaska, 4.7 in British Columbia, 4.7 in Oregon, and 5.4 in California), and if anything decreased slightly towards the north where one would expect the greatest overlap with the western population. The high nonpup to pup ratios indicate that high survival rather than high fecundity may be the primary mechanism responsible for population growth.

Steller sea lions in the eastern population currently breed at 13 major rookeries (>50 pups born), and the highest concentration of breeding animals is in southeastern Alaska, northern British Columbia, and near the Oregon-California border. Currently there is a large gap (993 km) between the Scott Islands rookery off northwestern Vancouver Island and the Orford and Rogue Reef rookeries in southern Oregon. There are no records of rookeries along this coastline, and natives hunting sea lions along the Washington coast had no knowledge of rookeries in that state (Scheffer, 1950). However, it would not be surprising to see new rookeries founded or re-established at haulout sites along this gap, as has occurred in southeastern Alaska, if the eastern population continues to increase in the northern part of its range. Nonbreeding animals use approximately 59 major haulout sites (>50 animals during) during the breeding season, plus numerous smaller sites and many seasonal haulout sites. The major haulouts are widely distributed from Cape Fairweather (58.8°N, 137.9°W) to Año Nuevo Island (37.1°N, 122.3°W), providing Steller sea lions with access to coastline spanning about 22° of latitude or 2400 km.

During the 1970s the eastern population represented only about 10% of the total number of Steller sea lions along the North American coast. With the large decline in the western population in conjunction with the increase in the east, this percentage has changed dramatically; about 55% of pup production in North America now occurs in the eastern population. We anticipate that continued monitoring and comparisons of the growing eastern population with the western population will provide insight into factors that ultimately regulate Steller sea lion populations, and we hope this synthesis for the eastern population will contribute toward better coordination of surveys and standardization of counting methods over the distribution range of the species.

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Appendix

Appendix Figure

Historic counts made over the last century of Steller sea lion (*Eumetopias jubatus*) pups (○), nonpups (●), and total number of animals (♦) at each breeding rookery within the range of the eastern Steller sea lion population.

Appendix Figure (continued)