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Preliminary Assessment of the Recovery Potential of Northern Fur Seals (*Callorhinus ursinus*) in British Columbia

Évaluation préliminaire du potentiel de rétablissement des otaries à fourrure du Nord (*Callorhinus ursinus*) de Colombie-Britannique

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ABSTRACT

The northern fur seal (*Callorhinus ursinus*) is the most abundant and widely distributed pinniped in the North Pacific Ocean. The species currently breeds on 6 rookeries, and although both sexes generally exhibit a high degree of fidelity to natal sites, there is sufficient exchange among sites to prevent genetic differentiation. Movements of animals between or colonization of new rookeries can affect population dynamics, so fur seals should be recognized as a single population. Pups are the only component of the population confined to land where they can be censused, and have been used to track population trends. Total pup production has declined by 38% over the last 30 years (3 generations) due to a decrease at the largest breeding site on the Pribilof Islands. Pup production at other rookeries has been stable or increasing, such that the proportion of pups born on the Pribilof Islands has dropped from 76% to 53% over the last 30 years. Due to the cessation of subadult male harvests on major rookeries, there has also been a shift in the sex- and age-structure of the population, from one skewed toward females to more natural sex ratio, resulting in a decrease in per capita pup production. Total population size is estimated to have dropped from 1.67 million to 1.22 million over the last 30 years, representing a decline of about 27% in total abundance, and a decline of about 23% in the number of mature individuals in the population.

Population projections for St. Paul Island suggest the Pribilof stock has been experiencing chronic declines since the 1950s. Females killed during a herd reduction program and taken for research accounted for 70% of the steep decline that occurred in the late 1950s and early 1960s, but models suggest that juvenile survival was below equilibrium levels and the population would have declined to some extent even in the absence of these kills (York and Hartley 1981; Trites and Larkin 1989). The reason for the lack of recovery from the herd reduction kills and for the continued decline is unknown. Simulations indicate a decline in pup production of the magnitude observed could result from juvenile survival remaining at 18% below equilibrium levels, an 8% decrease in adult survival, or a 12% decrease in pregnancy rate, all of which are biologically realistic but would be impossible to detect from data currently being collected. Following the termination of commercial subadult male harvests in 1984, the prevalence of adult males is projected to have increased sharply, but these predictions are difficult to validate as counts of idle and harem bulls provide only an index of their actual abundance. Given the larger size of males, the models indicate mean body mass has also increased, such that the biomass of fur seals in the Bering Sea may not have changed much over the last 30 years.

Northern fur seals wintering along the west coast of North America (California to SE Alaska) are comprised mainly of adult females (64%), with some juveniles (36%) and a few adult males (0.5%), representing about 74% of the adult female population and 52% of the entire population in the eastern Pacific Ocean. Seals arrive on the coast in December-January and depart in June-July, spending an average of 4.8 months in coastal waters. Overall abundance remains fairly stable from February-May, during which about 375,000 fur seals occupy coastal areas. The distribution of pelagic seals shifts northward along the coast during the winter, peaking off California in February, Washington in April, and British Columbia and SE Alaska in May. Roughly 123,000 fur seals inhabit Canadian waters at peak abundance in May, with highest densities on LaPerouse Bank off SW Vancouver Island. The main prey are northern anchovy and hake in the southern part of the wintering range, and herring, salmon and rockfish in the northern part, while squid is important in offshore areas.

The reasons for the decline of fur seals breeding on the Pribilof Islands is unknown. Only small numbers of subadult males are taken for subsistence and bycatch in fisheries is minimal, so

its unlikely direct human-induced mortality is driving the decline. Prey availability in the Bering Sea may have changed, perhaps due to changes in ocean conditions or as a result of commercial fisheries, as evident from declines of other pinnipeds in the Gulf of Alaska and Bering Sea (DeMaster *et al.* 2006). Female fur seals from the Pribilof Islands may also be experiencing greater intra- and inter-specific competition for prey resources. Relative numbers and biomass of male fur seals in the Bering Sea is predicted to have increased substantially since commercial harvests were terminated. California and Steller sea lions, which often feed on the same prey as northern fur seals, and have increased in abundance along the west coast of North America. The degree of competition between these apex predators warrants further study.

RÉSUMÉ

L'otarie à fourrure du Nord (*Callorhinus ursinus*) est le pinnipède le plus abondant et le plus largement dispersé dans tout le Pacifique Nord. L'espèce se reproduit actuellement dans six roqueries et, bien que les deux sexes se montrent très fidèles à leurs lieux d'origine respectifs, les échanges entre ces lieux demeurent suffisants pour éviter la différenciation génétique. Puisque les déplacements des otaries d'une roquerie à l'autre et la colonisation de nouvelles roqueries sont susceptibles d'affecter la dynamique des populations, il importe de reconnaître les otaries à fourrure comme une seule et même population. Les petits constituent le seul segment de population confiné au sol où il est possible d'en faire le recensement. Leur dénombrement sert depuis longtemps d'indice au suivi des tendances de la population. Le taux de natalité global des otaries à fourrure a chuté de 38 % en 30 ans (trois générations) en raison de la baisse dans la principale aire de reproduction des îles Pribilof. Dans les autres roqueries, le taux de natalité est demeuré stable, sinon en hausse, de sorte que la proportion des petits nés dans les îles Pribilof serait passée de 76 % à 53 % au cours des 30 dernières années. L'arrêt de la chasse des mâles préreproducteurs dans les principales roqueries produit des changements dans la structure par sexe et par âge de la population. D'une majorité de femelles, le rapport mâles-femelles de la population des otaries à fourrure est désormais mieux équilibré, entraînant une diminution de la production de petits par individu. L'on estime que la taille totale de la population est passée de 1,67 à 1,22 million otaries à fourrure ces 30 dernières années, ce qui représente un déclin d'environ 27 % de l'abondance de l'espèce et de 23 % du nombre d'individus adultes.

Les prévisions pour la population de l'île Saint-Paul semblent indiquer une diminution chronique du stock des îles Pribilof depuis les années 1950. Les femelles capturées dans le cadre d'un programme de réduction du troupeau et de la recherche expliquent l'important déclin de 70 % constaté entre la fin des années 1950 et le début des années 1960. Les modèles mathématiques ont toutefois indiqué un taux de survie inférieur à l'équilibre chez les juvéniles, qui aurait entraîné une certaine diminution de la population même en l'absence de cette chasse (York et Hartley, 1981; Trites et Larkin, 1989). La faiblesse du rétablissement subséquent et le déclin soutenu de l'espèce demeurent inexpliqués. Des calculs par simulation ont montré qu'une réduction dans la production de petits de cette ampleur pourrait être attribuable à un taux de survie des juvéniles inférieur de 18 % au point d'équilibre, à une réduction de celui des adultes de 8 % ou à une diminution de 12 % du taux de gravidité. Quoique biologiquement réalistes, ces conclusions sont toutefois impossibles à vérifier à partir des données actuellement recueillies. L'on estime que le nombre de mâles adultes aurait connu un essor considérable suivant l'interdiction, en 1984, de la récolte commerciale des mâles immatures, mais ces estimations sont difficiles à valider puisque le dénombrement des mâles vivant au sein des harems et des mâles sans partenaire sexuel ne fournit qu'un indice de leur abondance actuelle. Puisque les mâles ont une plus grande taille que les femelles, les modèles mathématiques indiquent également une augmentation de la masse corporelle moyenne. La biomasse des otaries à fourrure pourrait donc être demeurée sensiblement la même dans la mer de Béring depuis 30 ans.

La population d'otaries à fourrure du Nord hivernant le long de la côte ouest de l'Amérique du Nord (de la Californie au sud-est de l'Alaska) est surtout composée de femelles adultes (64 %), de quelques juvéniles (36 %) et mâles adultes (0,5 %), qui représentent environ 74 % de la population des femelles adultes et 52 % de la population totale de l'est de l'océan Pacifique. Les otaries rejoignent les côtes en décembre-janvier pour regagner la mer en juin-juillet, passant une moyenne de 4,8 mois en eaux côtières. Dans l'ensemble, l'abondance demeure relativement stable de février à mai où l'on dénombre près de 375 000 otaries à fourrure sur les côtes. En saison hivernale, l'aire de répartition des otaries pélagiques les amène à se déplacer vers le nord,

le long des côtes; elles se rassemblent ainsi en Californie en février, dans l'État de Washington en avril, puis en Colombie-Britannique et dans le sud-est de l'Alaska en mai. Au sommet de leur abondance, en mai, près de 123 000 otaries à fourrure fréquentent les eaux canadiennes, la plus forte densité étant observée sur le banc LaPerouse, au large du sud-ouest de l'île de Vancouver. Leurs proies principales sont l'anchois du Pacifique et le merlu dans la partie sud de leur trajet migratoire, ainsi que le hareng, le saumon et le sébaste dans la partie nord, tandis que le calmar constitue une source de nourriture importante dans les eaux hauturières.

Le déclin du taux de reproduction des otaries à fourrure dans les îles Pribilof demeure inexpliqué. Seule une très petite quantité de mâles préreproducteurs est chassée à des fins de subsistance et le nombre de captures accessoires des pêches est relativement minime. Il est donc peu probable que le taux de mortalité directement causé par l'homme puisse être un important facteur de ce déclin. La disponibilité des proies dans la mer de Béring pourrait avoir connu certaines fluctuations, répercussion possible de changements survenus dans le milieu océanique ou des pêches commerciales, comme en témoigne la diminution d'abondance d'autres pinnipèdes du golfe d'Alaska et de la mer de Béring (DeMaster et coll., 2006). Les otaries à fourrure femelles des îles Pribilof pourraient également être victimes d'une concurrence intra ou interspécifique pour les mêmes proies. L'on estime que le nombre relatif et la biomasse des otaries à fourrure mâles dans la mer de Béring aurait connu un essor considérable suivant l'interdiction de la chasse commerciale. L'otarie de Californie et l'otarie de Steller, qui se nourrissent souvent des mêmes proies que l'otarie à fourrure du Nord, ont augmenté en abondance le long de la côte ouest d'Amérique du Nord. Le degré de concurrence entre ces prédateurs du sommet de la chaîne alimentaire justifie une étude plus approfondie.

INTRODUCTION

In 1996 and 2003, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) reviewed the status of northern fur seals in Canada and concluded they were *not at risk* of extinction (Baird and Hansen 1997; COSEWIC 2003a). In April, 2006, COSEWIC re-evaluated their status (Willis and Trites 2006) and recommended they be listed as *threatened* under SARA. The recommendation to change the status was made on the basis of a 54% decline in the number of pups counted on the Pribilof Islands – the largest fur seal rookery in the North Pacific Ocean and origin of most fur seals occurring in Canadian waters – over a 30 year (3 generations) period, 1974-2004. The extent of the decline warranted an *endangered* listing based on COSEWIC criteria, but given its large population size and that it had recovered from low levels in the past, the recommendation was downgraded to *threatened*. Such a designation implies a risk of extinction of about 10% within the next 100 years if the threatening factors are not mitigated.

DFO has established a Recovery Potential Assessment (RPA) process to provide information and scientific advice for meeting SARA requirements for listed species, and for deciding whether to add species that COSEWIC recommends be listed (DFO 2006). The RPA is intended to help define the status of the species, establish targets and a time frame for recovery, and evaluate the uncertainty associated with management actions. Ideally, the RPA should assess present and recent trends in abundance and distribution, and describe the characteristics and availability of critical habitat. To the extent possible, the RPA should also evaluate impacts of human-induced mortality by determining sustainable levels and quantifying the individual sources and aggregate of such mortality. Finally, the RPA should identify means of mitigating or minimizing human-induced mortality and threats to critical habitat.

For northern fur seals, the specific cause of the declines and limiting factors have not been identified. Moreover, there are presently no known sources of direct human-induced mortality in Canadian waters, and only a small subsistence harvest of surplus males and minimal bycatch in fisheries, neither of which are considered to be having a significant impact on populations (Angliss and Outlaw 2007; NMFS 2006). Consequently, previous assessments of threats and limiting factors have tended to focus on indirect ecosystem processes, such as bottom-up forcing due to prey limitation, or top-down forcing due to increased levels of predation by killer whales (NMFS 2006; Willis and Trites 2006). This necessitates a broader and somewhat more exploratory analysis of the factors that might indirectly influence the recovery potential of northern fur seals.

This Research Document is intended to provide the scientific basis for developing a RPA for northern fur seals. The report consists of three Sections. Section 1 provides a brief overview of the general biology of northern fur seals, reviews historic and recent counts and estimates of pup production, and summarizes information on dispersal of animals between rookeries. Multipliers derived from life tables are applied to estimate total abundance and the approximate number of mature individuals in the population. The main objective was to assess the geographic scope, magnitude and timing of the population declines, so as to identify an appropriate scale for assessing status and delineating recovery targets.

In Section 2, projection models are used to examine the population dynamics of northern fur seals on St. Paul Island, the largest breeding rookery and focus of many previous studies, and the origin of most animals wintering in Canadian waters. COSEWIC guidelines stipulate that the status of a species be evaluated on the basis of the number of mature individuals in populations

(COSEWIC 2003b), but for fur seals the only component of the population confined to land where they can be reliably counted are pups, so population models need to be applied to estimate the prevalence of older animals (Berkson and DeMaster 1985). Moreover, northern fur seals segregate by sex and age during their migration, so information on the sex- and age-structure of the population is required for estimating abundance in Canadian waters. Applying multipliers and inferring population structure of the Pribilof Island stock is complicated by the fact that selective harvests and reduction programs altered the sex- and age-composition of the population, such that the multipliers have changed over time (Loughlin *et al.* 1994).

Section 3 describes the migration patterns of northern fur seals along the west coast of North America (California to SE Alaska), particularly off British Columbia. The observed sex and age-composition of fur seal specimens collected along the west coast is compared with the overall sex- and age-composition of the population to determine the segment wintering in coastal waters. I also examine historic sealing records, and fur seal sightings and specimens collected during pelagic research trips, to determine the seasonal distribution and diet of fur seals wintering along the west coast, particularly off British Columbia. The main objective was to identify habitat requirements and gain a better understanding of potential threats or limiting factors in Canadian waters. I also compared the population trends of northern fur seals with trends of other pinnipeds on the west coast to determine if the trajectories were similar, as in the Gulf of Alaska and Bering Sea, suggesting that a common element may be impacting all pinnipeds (Springer *et al.* 2003; DeMaster *et al.* 2006; Wade *et al.* in press). Information on where and when fur seals occur in Canadian waters and what they feed on will also facilitate a socio-economic assessment of the implications associated with listing fur seals under SARA.

1. BACKGROUND AND POPULATION STATUS

1.1 General Biology

The genus *Callorhinus* contains one species, the northern fur seal, *C. ursinus* (Scheffer 1958; Rice 1998). There is little evidence of genetic differentiation among breeding sites (Rice 1998; Ream 2002) and since considerable interchange of individuals takes place between rookeries, northern fur seals are considered to comprise a single population (Rice 1998; NMFS 2006). For management purposes, rookeries or adjacent rookeries are considered separate stocks. Two stocks are recognized in U.S. waters: the Eastern Pacific stock (Pribilof and Bogoslof Islands) and the San Miguel Island stock (Carretta *et al.* 2007; Angliss and Outlaw 2007). Separation of the two stocks is based on the Dizon *et al.* (1992) phylogeographic approach: 1) distributional data: geographic distribution is continuous during feeding, geographic separation during the breeding season, high natal site fidelity (Baker *et al.* 1995; DeLong 1982); 2) population response data: substantial differences in population dynamics between Pribilof, Bogoslof and San Miguel Islands (DeLong 1982, DeLong and Antonelis 1991, NMFS 1993, Ream *et al.* 1999); 3) phenotypic data: unknown and 4) genotypic data: little evidence of genetic differentiation among breeding islands that have been compared (Ream 2002).

The northern fur seal is a rather small pinniped, but exhibits extreme sexual dimorphism. Pups are black and average about 5.2-5.9 kg at birth (Scheffer and Wilke 1953; Trites 1991), but more than triple in body mass during a 4 month nursing period, by which time they weigh about a third as much as their mothers (Gentry 1998). Adult females typically weigh 35-45 kg, with most growth having been completed by 5 years of age (Lander 1980b; Trites and Bigg 1996). Males continue to growth until about 10 years of age, typically attaining a body mass of 150-200 kg, with the largest territorial males weighing just over 300 kg (Lander 1981; Gentry 1998). The pelage of females is gray-brown along the dorsal surface and lighter along the underbelly, and that of males varies from black to reddish brown with a mane over the shoulders. The underfur is brown for both sexes but is not visible on dry animals, and appears as brown streaks on wet animals. Females typically mature at 4-6 years of age (York 1983; Trites and York 1993) with pregnancy rates varying from 75-90% for females in their reproductive prime between 8-13 years of age, with older animals exhibiting reproductive senescence (Lander 1981; York and Hartley 1981; Trites and York 1993). Female longevity may exceed 25 years, but due to high mortality of juveniles, mean life expectancy in a stable population was estimated to be about 5.1 years, and generation time about 10 years. Maximum longevity of males may extend exceed 15 years, with a mean life expectancy of roughly 3.3 years[1] (Olesiuk, unpublished life table analyses, based on Lander (1981); Section 2.2).

The life cycle consists of a 4-5 month breeding season during which mature animals come ashore at rookeries to give birth, nurse young and mate, followed by 7-8 month pelagic phase. Northern fur seals currently breed on 6 rookeries (Figure 1), with the 5 largest breeding areas located between 48ºN to 57ºN latitude in the Bering Sea, Sea of Okhotsk and Gulf of Alaska, with one small rookery on San Miguel Island at 34ºN latitude off California. The breeding season begins in May with the arrival of males, which stake out territories that will be defended for typically 38-42 days (up to 87 days) while fasting (Gentry 1998; Gentry 2002). Males aged approximately 7+ years compete for territories at breeding areas occupied by females (harem bulls), or maintain territories without females on the periphery (idle bulls) but may play an important role in mating younger females (Gentry 1998). The breeding system is highly polygynous, with ratios of harem bulls to females ranging from about 9:1 in a natural population, to as high as 60:1 when males are heavily harvested, apparently with little effect on pregnancy rates (Gentry 1998; Gentry 2002). Females arrive on rookeries in late June or July in decreasing order of age and given birth to a single pup within a day or two. Mothers remain on land with the newborn pup for about a week, and mate 3-8 days after parturition (Petersen 1968; Gentry 1998). Females subsequently make a series of foraging trips lasting 4-10 days (varying with location and local typography; Gentry 1998), punctuated with 1-2 day visits on land to nurse pups. The foraging trips continue until pups are weaned at about 4 months of age in November. Prey resources within the commuting distance of females are probably a crucial feature of breeding sites (Gentry 1998).

After breeding, animals undertake a 7-8 month pelagic migration (Kenyon and Wilke 1953; Bigg 1990). Pups depart from rookeries after being weaned in November, traveling southward and leaving the Bering sea during December (Ragen *et al.* 1995). Immature animals become widely distributed and tend to remain at sea during the first 2-3 years of life (Townsend 1899; Manzer *et al.* 1969; Bigg 1990). Adult males tend to winter at northerly latitudes in the Bering Sea, Sea of Ohtosk, or Gulf of Alaska (Kajimura 1980; Loughlin *et al.* 1993). Adult females tend to winter in coastal areas over the continental shelf or along the shelf break (Bigg 1990), but the subarctic-subtropical transition zone also appears to be an important wintering area (Ream *et al.* 2005) and may serve as a southern barrier for prey species (Sinclair 1990; Beamish *et al.* 1999; Ream *et al.* 2005). Further details for migration patterns along the west coast of North America and coastal waters off British Columbia are provided in Section 3. Animals may occasionally haul out during the non-breeding season (Fiscus 1983), but sightings or reports of animals on land in British Columbia are rare (Olesiuk, unpublished data).

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[1] During subadult males harvests, mean life expectancy had been reduced to as low as 2.5 years, as males experience high natural mortality over the first 2 years of life, and then a high proportion were subsequently harvested when they began to return to rookeries at 3-5 years of age.

1.2 Historic Abundance and Distribution

Historic estimates of abundance are somewhat uncertain, but based on numbers of pelts taken its been estimated there may have been 2-3 million northern fur seals when the first breeding site was discovered in 1742 (Gentry 1998). The species appears to have undergone 3 periods of depletion (Gentry 1998). The first depletion began with the discovery of the Commander Island rookeries in 1742, and the Pribilof Islands in 1786-87. Unregulated hunting decimated populations by the early 1800s (Stejneger 1896, 1925, both cited in Gentry 1998). The declines led Russian authorities to impose the first regulations on the harvest, which prohibited the taking of females on the Pribilof Islands in about 1834 (but not enforced until 1847; Elliot 1884 in Gentry 1998) and the Commander Islands in about 1843 (Stejneger 1896, cited in Gentry 1998; Lander 1980a). Thus began a long history of selective harvests of subadult males, most aged 3-5 years as they began returning to breeding sites. The management strategy, apparently devised by Russian sealers, was to remove surplus males, leaving only the number required for reproduction in this highly polygynous species (Roppel and Davey 1965; Roppel 1984). Under this regime, the rookeries at Pribilof Island stock recovered over the next 5 decades, from perhaps 300,000 to about 2.1 million (Lander 1980a, NMFS 1993; Gentry 1998). The Commander Island stock also increased during this period, such that fur seal abundance had probably recovered to near historic levels by the late 1870s (Gentry 1998).

The second major depletion was caused by unregulated hunting of seals at sea. Pelagic sealing began in about 1868, peaked in 1892-94 (61,838 skins taken in 1894; Baker *et al.* 1970 cited in Murie 1981), and continued until 1910 (Townsend 1899; Murie 1981). Schooners made trips lasting many months or an entire year, and hunted seals with rifles or spears from small skiffs or canoes launched from the schooners (Murie 1981). The sealing fleet targeted the high densities of seals wintering in coastal areas on both sides of the Pacific Ocean, and followed migrating seals back to breeding sites in the Bering Sea and Sea of Okhotsk. Initially, the only regulation was seals could not be hunted within 60 nm of the Pribilof Islands. In 1897, American citizens were prohibited form hunting seals in the Bering Sea, after an earlier effort to ban all pelagic sealing had failed (Murie 1981; Roppel and Davey 1965). This created a monopoly for Canadian-registered vessels and Victoria, British Columbia, emerged as the centre of the sealing industry (Murie 1981), joined later in the early 1900s by Japanese vessels (Roppel and Davey 1965). The Victoria Sealing Company harvested an estimated 255,000 seals during 1886-1911, accounting for the vast majority of the pelagic take after 1894. Reliable information on the sex- and age-composition of the pelagic harvest is not available (Murie 1981), but judging from what we now know about migration patterns (Section 3.3), a high proportion of seals taken in coastal areas were likely reproductive females. Pelagic sealing, attenuated by a large unregulated kill on the Pribilof Islands following the transfer of possession from Russia to United States, decimated the fur seal population, leading to the signing of the North Pacific Fur Seal Treaty in 1911 which prohibited pelagic sealing.

There also appears to have been major shifts in breeding distribution of northern fur seals over their history. The species is believed to have been in existence for about 5 million years (Gentry 1998), whereas the Pribilof Islands formed only about 2.2 million years ago (Cox *et al.* 1966 cited in Gentry 1998), and have been repeatedly inundated by or isolated from the ocean over the last 250,000 years due to inter-glacial sea level changes (Hopkins and Einarsson 1966 and Hopkins 1973, both cited in Gentry 1998). Northern fur seals, including the remains of newborn animals and adults of both sexes, which implies breeding activity, are common in archeological sites in California, Oregon, Washington and British Columbia (Gustafson 1968; Lyman 1988; Crockford *et al.* 2002). Its possible fur seal breeding sites once ranged as far south as Baja California (Davies 1958). Orr (1972) speculated that northern fur seals may have at one time had a coastal breeding range somewhat like the present day breeding range of Steller sea lions.

1.3 Recent Trends in Pup Production

Population assessments for northern fur seals, like many other pinnipeds, have been based on pup counts, as pups are the only segment of the population that are accessible on land and can be censused at any given time (Berkson and DeMaster 1985). Various methods have been used to estimate the number of fur seal pups born based on direct counts, densities, or mark-recapture of tagged or marked (sheared) pups (Lander 1980a; York and Kozloff 1987; York 2005a). Recent estimates of pup production (counts or estimates of live and dead pups) for each breeding site are summarized in Figure 2, which are used here to assess the extent of the decline in northern fur seal abundance and number of mature individuals, particularly over the 30 years (3 generations).

The Pribilof Islands supports the largest breeding aggregation of northern fur seals. York (2005a) provided a summary of pup counts for the Pribilof Islands and how census techniques have evolved since the U.S. took possession in 1867. Following the termination of pelagic sealing in 1911, pup production on the Pribilof Islands began to recover at close to the expected maximum intrinsic rate of 8% (Figure 2a). However, by the late 1940s, it was apparent that the growth rate had slowed and harvests were falling below expectations. It was suggested that reproductive and juvenile survival rates had been depressed due to rising competition for prey resources around the Pribilof Islands (Kenyon *et al.* 1954; Chapman 1961). Mathematical models predicted that productivity could be enhanced and a higher sustainable harvest achieved from a smaller population (Anonymous 1955; Chapman 1961; Nagasaki 1961). This led to a herd production program during 1956-68, in which nearly 300,000 females were killed on the Pribilof Islands (York and Hartley 1981). During 1958-74, an additional 16,000 females were collected at sea in the eastern Pacific and Bering Sea by Canada and the U.S. as part of a scientific research being conducted under the auspices of the North Pacific Fur Seal Commission (Lander 1980b). These kills precipitated the third and most recent period of decline (Gentry 1998). Projection models indicated that the female removals accounted for about 70% of the decline in pup production observed during the 1960s and 1970s (York and Hartley 1981). The remaining 30% was attributable to biases in pup estimation techniques or juvenile survival rates being below equilibrium levels (York and Hartley 1981; Trites 1984[2]; Trites and Larkin 1989). Unexpectedly, the Pribilof Island stock did not exhibit the increase in productivity anticipated following the herd production, and pup production continued to decline (Trites and Larkin 1989). The decline may have been interrupted by a period of stability in the 1980s, but has resumed in recent years (Figure 2a) (Towell *et al.* 2006; Towell and Fowler 2007). During the last 30 years, pup production on St. George Island has declined by an average of about 3.2% (r^2=0.95; $F_{1,13}$=113.9; P<0.001) and on St. Paul it has declined at about 2.0% (r^2=0.82; $F_{1,21}$=44.4; P<0.001). Since it was these declines that led to the COSEWIC recommendation to list northern fur seals (Willis

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[2] Trites, A. W. 1984. Stock assessment and modeling of the North Pacific fur seal population. Unpublished Report. DFO Contract #OST83-00133. 82p.

and Trites 2006), I examine their dynamics and the demographic changes that may have caused them in greater detail in Section 2.

Boltnev (1996) and Burkanov and Calkins (2007) provided overviews of the status of northern fur seals in the Commander Islands, the second largest breeding aggregation. Like other rookeries, this stock had been depleted by pelagic sealing. Pup surveys began in the late 1950s and indicated that pup production increased from about 38,000 in the late 1950s to a peak of about 75,000 in the mid-1970s, representing an annual growth rate of 2.8% (Figure 2b). Pup production began to decrease in the late 1980s, but the variability of counts and increasing number of bachelor males led Burkanov and Calkins (2007) to suggest total population size may actually have been stable or increasing. The most recent ground count in 2006 indicated 59,805 pups were present. Based on an examination of all available counts and local knowledge of fur seal distribution on the Commander Islands, Burkanov and Calkins (2007) concluded that pup production may have decreased slightly between the late-1980s and mid-1990s, but had since stabilized. Overall, there has been little net change in pup production on the Commander Islands over the last 30 years.

The early pup counts for Robben Island (Lander 1980a) indicated that fur seals were recovering from pelagic sealing during the early 1900s, attaining a peak count of 56,040 in 1967 (Figure 2c). For reasons unknown (only a few females were killed accidentally during commercial harvests in the 1960s, and small numbers were taken in experimental kills in the 1970s; Lander 1980a), pup production subsequently declined, with the low count of 17,804 in 1986. This spontaneous decline led Gentry (1998) to suggest that the factors causing the decline of the Pribilof Island stocks were operating at a broader scale, although the Robben Island decline seems to have begun at least a decade later. Moreover, the most recent pup counts of 26,400 in 2002 (Kurzin pers. comm., cited in NMFS 2006) and about 30,000 in 2005 indicate that the Robben Island stock has probably increased during the past decade (V. Burkanov, NMML and ASLC, pers. comm.). Overall, there has been little net change in pup production on Robben Island over the last 30 years.

Bukanov *et al.* (2007) provided an account of the status of northern fur seals in the Kurile Islands. Historically, northern fur seals were widely distributed in the Kurile Islands, utilizing 9-10 rookeries, but uncontrolled harvesting in the 19th century was thought to have eradicated the species from the area until a small breeding colony with about a thousand pups was discovered in 1955-56. Regular surveys were initiated in 1962, and pup production increased rapidly (20% per annum) until 1977, but appeared to have stabilized by 1988 when surveys were suspended (Figure 2d). The most recent spook counts in 2005 and 2006 were 30,192 and 27,090 pups respectively, indicating that pup production in the Kurile Islands has continued to increase (Burkanov *et al.* 2007). During the last 30 years, pup production has increased significantly (r^2=0.74; $F_{1,13}$=16.2; P<0.001) at an average rate of about 2.3% per annum.

Small numbers of fur seals were first observed on Bogoslof Island in the late 1970s (Loughlin and Miller 1989), and the first instances of pupping were recorded in 1980 (Lloyd *et al.* 1981). The rookery expanded rapidly through the 1980s and 1990s (Figure 2e) (Ream *et al.* 1999; NMFS 2006), at a growth rate almost double the maximum intrinsic rate of 8% (r^2=0.97; $F_{1,7}$=126.1; P<0.001). This new rookery now produces nearly 10% as many pups as the Pribilof Islands.

After an absence of at least a thousand years (Walker 1979), northern fur seals began breeding at San Miguel Island in the Channel Islands in 1960s, and the colony grew rapidly in the

1970s (DeLong 1982). However, recent increases have been interspersed with major declines in pup production in 1983 and 1998, and a smaller decline in 1991 (Figure 2f). The episodic declines corresponded with the major *El Nino* events of 1982-83 and 1997-98 and a mild *El Nino* event in 1992-93, which affect prey abundance and can result in nearly complete loss of fur seal cohorts and in some cases elevated mortality of older age-classes (DeLong and Antonelis 1991; Melin and DeLong 1994; Melin *et al.* 1996; Melin and DeLong 2000). A few fur seals tagged on San Miguel Island have recently been sighted breeding on the Farallon Islands (Pyle *et al.* 2001).

Overall changes in pup production over the last 30 years (3 generations) were examined by comparing counts during the most recent 5-years (2002-2006) with the corresponding period 30 years earlier (1972-1976). Pooling over 5-year periods is advantageous in that it allows several counts to be averaged, particularly the 3 most recent biennial surveys on the Pribilof Islands, rather than relying on any single count (Loughlin *et al.* 1994). Pooling also circumvents the problems associated with the fact that not all rookeries were surveyed in exactly the same years. Total pup production of northern fur seals on all breeding sites was estimated to have declined from about 454,000 pups in 1972-76, to 282,000 pups during 2002-06, representing a decline of 38% (Table 1). Essentially all of the decrease occurred on the Pribilof Islands. Pup production on all other rookeries combined had actually increased by about 20% over the last 3 decades, and no other rookery has exhibited the sustained declines seen on the Pribilof Islands. Consequently, the proportion of total pup production born on the Pribilof Islands dropped from 76% in 1972-76 to 53% by 2002-06. The new rookeries established on the Kurile Islands in the 1950s, on San Miguel Island in the 1960s, and on Bogoslof Island in the 1980s, collectively accounted for about 15% of total pup production during 2002-2006, compared with 2% during 1972-76.

While northern fur seals generally exhibit a high degree of site fidelity, there is also considerable exchange of both males and females among rookeries. Movements are evident from resightings and recoveries of tagged animals, but precise estimates of emigration and immigration rates are difficult to estimate due to the regional disparities in tagging and recovery effort. In particular, there was a massive tagging program on Pribilof Islands, where over 0.7 million tags were deployed, primarily for mark-capture estimates of pup production (York 2005b). There was little systematic effort to monitor dispersal to other sites, and most returns came from harvests, which were highly biased toward sub-adult males aged 2-5 years at the rookeries being harvested. Smaller numbers of tags were recovered from pelagic collections, which tend to be biased toward adult females in coastal areas (see Section 3.1). Nevertheless, the tag recoveries provide a general sense of the degree of dispersal among breeding stocks.

On the Pribilof Islands, where most of the tags had been deployed, less than 1% of the harvested sub-adult males with tags had been tagged elsewhere, primarily the Commander Islands, and rarely Robben Island (Lander and Kajimura 1982). In contrast, on the Commander Islands in the 1970s, it was estimated that 12-21% of the tagged males harvested had originated from the Pribilof Islands, 0.1-0.5% from Robben Island, and the remaining 82-88% from the Commander Islands. An estimated 93% of subadult males killed on Robben Island originated there, with 1.3-5.0% tagged on the Pribilof Islands and 0.3-1.9% on the Commander Islands.

Evidence of female dispersal from natal breeding sites comes mainly from the formation of new or re-colonization of former rookeries in recent years. Mainly seals from the Commander and Robben Islands contributed to the re-population of the Kurile Islands, but a few tagged animals from the Pribilof Islands have also been sighted there (Lander and Kajimura 1982). The northern fur seals that re-colonized San Miguel Island in the California Channel Islands during the 1950s or early 1960s were immigrants from the Pribilof Islands and Commander Islands, but apparently included at least one animal from Robben Island (Peterson *et al.* 1968; DeLong 1982; Antonelis *et al.* 1988). Its assumed the rapid expansion of the Bogoslof Island rookery is being driven largely by female immigrants from the Pribilof Islands Ream *et al.* (1999). The general pattern seems to be one of dispersal from larger rookeries to smaller or new rookeries, but its not clear to what extent this may be biased by disparities in tagging effort, with most tags being deployed at the larger sites, particularly the Pribilof Islands. Immigration from other rookeries can thus contribute to the dynamics of smaller rookeries (Frisman *et al.* 1982), but as Gentry (1998) noted, emigration alone cannot fully account for the magnitude of declines observed on the large rookeries at Robben Island during the 1970s, or the recent declines on the Pribilof Islands.

1.4 Recent Changes in Abundance

Pup counts provide an index of changes in relative abundance, but COSEWIC listing criteria are based on the absolute number of mature individuals in populations (COSEWIC 2003b). Life table analyses can be used to determine the sex- and age-structure of the population, which can be used to derive multipliers based on the ratio of the total number of animals (or segment of interest) to the number of pups born (Berkson and DeMaster 1985). For northern fur seals, this procedure is somewhat complicated by the fact that the sex and age-structure of some stocks was altered by sex- or age-selective kills, such that multipliers sometimes changed over time (Loughlin *et al.* 1994; York 2005a), and different multipliers may be appropriate for different rookeries depending on the history of harvests.

York (2005a) summarized the derivation and evolution of multipliers for the Pribilof Island stock (Table 2). The earliest attempt to extrapolate abundance from pup counts was by Osgood *et al.* (1915 cited in York 2005a), based on the simplistic assumption that the number of adult females in the population was equal to the number of pups counted, which implied all 3+ females were pregnant. Kenyon *et al.* (1954) derived a more realistic ratio of 3.34 based on an analysis of pregnancy and survival rates from the early pelagic data. This was similar to the 3.37 calculated by Lander (1981) using life tables based on mortality and pregnancy rates from the entire pelagic sample, and samples of males collected on land (Table 2). These ratios were derived during a period of heavy exploitation on the Pribilof Island stock in which most subadult males were being killed. Subadult males at the two other major rookeries on the Commander and Robben Islands were also being harvested at similar rates leading up to the 1972-76 period. During 1960-72, the number of males harvested on the Commander Islands was 18% the number taken on the Pribilof Islands, whereas pup production on the Commander Islands was about 17% the levels on the Pribilof Islands. On Robben Island, the male harvest during the same period averaged about 16% of the Pribilof Island harvest, whereas pup production was about 13% of the levels on the Pribilof Islands. I therefore applied Lander's (1981) multiplier of 3.37 to each of these 3 heavily harvested stocks to estimate abundance for the 1972-76 period.

With the cessation of the commercial male harvests, a higher proportion of subadult males survived adolescence and were recruited to the adult male population. Loughlin *et al.* (1994) adapted the life tables developed by Lander (1981), which included both harvesting and natural mortality for males, for an unexploited population, which gave a multiplier of 4.47 (Table 2). The increase was due primarily to a nearly 5-fold increase in males aged 6+ years. Since most males were harvested at 3-5 years of age, and the bulk of adult males in an unharvested population are aged 6-12 years, the transition from a harvested to natural male age-structure takes roughly a decade after the harvest is terminated (see Section 2.2; Figure 5b). Since the large harvests of males ended on the Robben and Commander Islands in the early-mid 1970s, I applied the Loughlin *et al.* (1994) multiplier for unexploited populations to these stocks during 2002-2006. I applied the same multiplier to Bogoslof and Kurile Island rookeries for both periods, since neither had ever been harvested. For the Pribilof Islands, where male harvests were terminated on St. George Island in 1972 and on St. Paul in 1984, I used a slightly revised multiplier based on the population projections for St. Paul Island (Section 2.2), which predicted the multiplier increased from 3.5.-3.8 during 1972-76 to 4.1-4.4 during 2001-2006. These values tend to be marginally less than the Lander (1981) and Loughlin *et al.* (1994) multipliers, largely because pup production (i.e. the initial size of cohorts) was decreasing over time, such that the population was skewed toward older animals. In contrast, the Lander (1981) and Loughlin *et al.* (1994) life tables both imply a stationary population. For the small stock breeding on San Miguel Island, I used DeLong's (1982) multiplier of 4.0, which he deemed more appropriate based on the age-structure of immigrants to this small population.

Applying these multipliers to the estimates of pup production (Section 1.3), its estimated that total abundance of northern fur seals declined from approximately 1.67 million in 1972-1976 to 1.22 million in 2002-2006, representing a 27% decline over the last 30 years (3 generations) (Table 3). This is less than 38% in decline of pup production because the composition of the largest herds had shifted toward older animals since the commercial harvests were terminated. Using the abundance of age 4+ females and age 6+ males as an index of adult population size, the total number of mature individuals in the population is estimated to have declined by 23% over the last 30 years (3 generations), which is again less than the decline in pup or total abundance due to the increased prevalence of adult males. The mean body mass of individuals is also predicted to have increased with the shift toward more older animals, from 21.6 kg in 1972-1976 to 28.9 kg in 2002-2006. Interestingly, the predicted increase in mean body mass was about the same magnitude as the decline in total abundance, suggesting that the biomass of northern fur seals may not have changed much over the last 30 years, which might be a more relevant metric from an ecological perspective.

Despite the recent declines on the Pribilof Islands, northern fur seals continue to be the most abundant pinniped in the North Pacific Ocean, outnumbering all other species combined (Table 4).

1.5 Potential Threats and Limiting Factors

The underlying cause(s) of the declines of the Pribilof Island fur seal stock have not been identified. There are no known sources of direct human-induced mortality of sufficient magnitude to be causing, or even significantly contributing, to the decline. The large commercial harvests were terminated on St. George Island in 1972, and on St. Paul Island in 1984 (NMFS 2006). There is still a small subsistence harvest of subadult males, but recent takes have been low (average of 754 during 2000-2004; Angliss and Outlaw 2007), and there is little evidence that the much larger commercial harvests of subadult males in the past had any adverse effect on reproductive rates (Gentry 1998). Indeed, fur seal herds generally flourished during periods of male harvesting, whereas the declines are associated with kills of females (Roppel and Davey 1965; Scheffer *et al.* 1984; Gentry 1998). Although a few females have occasionally been included in subsistence harvest, none are known to have been taken since the late 1990s (Angliss and Outlaw 2007). Subsistence hunting of fur seals is known to occur in other parts of Alaska, but takes are believed to be minimal (NMFS unpubl. data, National Marine Mammal Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115, cited in Angliss and Outlaw 2007). No commercial or subsistence harvesting is known to occur in Canadian waters.

A small number of northern fur seals are killed incidentally during fishing operations. An estimated 246 northern fur seals were killed incidentally in the foreign and joint ground fish trawl fisheries in the North Pacific from 1978 to 1988, representing a mean annual kill of 22 seals (Perez and Loughlin 1991). Hobbs and Jones (1993) estimated that 1,579-1,927 fur seals were incidentally killed in 1989 and 4,960 in 1990 in the high-seas squid fishery. Based on the timing and location of these kills, the bycatch was likely comprised mainly of juvenile fur seals. The foreign high seas driftnet fisheries also incidentally killed large numbers of northern fur seals, with an estimated 5,200 animals taken during 1991 (Larntz and Garrott 1993). In 1992, commercial drift-net fishing in the North Pacific was halted as a result of a 1991 United Nations resolution that called for a global moratorium on large-scale high-seas drift-net fishing, although some low level of illegal fishing may still be occurring. Currently, the only federally observed fishery in the U.S. in which incidental mortality was documented was the Bering Sea and Aleutian Islands flatfish trawl (mean annual mortality of 0.48; Perez in review, cited in Angliss and Outlaw 2007). Observer programs for five other Alaska commercial fisheries have not documented any takes of fur seals. Observer programs for Canadian fisheries on west coast are not as extensive, but fishing operations are somewhat similar, so few if any fur seals are likely taken. Commercial net fisheries in international waters of the North Pacific Ocean have decreased significantly in recent years. The assumed level of incidental catch of northern fur seals in those fisheries, though somewhat uncertain, is thought to be minimal (T. Loughlin, NMFS-NMML, pers. comm., cited in Angliss and Outlaw 2007).

Mortality resulting from entanglement in marine debris was implicated as a contributing factor in the decline of the northern fur seal population on the Pribilof Islands during the 1970s and early 1980s (Fowler 1987, Swartzman *et al.* 1990, Fowler 2002). Surveys conducted from 1995 to 1997 on St. Paul Island indicate a rate of entanglement among subadult males comparable to the 0.2% observed from 1988 to 1992 (Fowler and Ragen 1990; Fowler *et al.* 1994), which is lower than the 0.4% observed during 1976-85 (DeLong *et al.* 1988; Fowler *et al.* 1994). Entanglement rates of male northern fur seals on St. Paul from 1998 to 2002 were 0.20, 0.26, 0.25, 0.30, and 0.37 (Zavadil *et al.* 2003). The recent rates of entanglements are close to those recorded in the mid-1980s; however, recent changes in methodology (counting juvenile males vs. all males) make direct comparisons between recent and historical data difficult (Zavadil *et al.* 2003). In 2002, the composition of entangling debris switched from predominantly packing bands to trawl net fragments (Zavadil *et al.* 2003). Entanglement rates appear to be much lower for females, but its not known whether this indicates whether fewer get entangled, or whether fewer entangled females survive. Although the proportion of entangled animals on land is insufficient to account for recent declines, the number of animals becoming entangled and dying at sea could potentially be a significant factor (Laist 1997). Fowler (1982, 1987) estimated entanglement mortality could be as high as 15% for seals from birth to 3 years of age, which (if equally distributed between both sexes) is close to the decrease in juvenile survival necessary to cause the observed rate of decline in pup production (Section 2.2).

Environmental contaminants such as heavy metals, organochlorines (e.g. DDT, dioxins and furans) and polychorinated biphenyls (PCBs) bioaccumulate through marine food chains, and in some cases high levels have been reported in northern fur seals (Tanabe *et al.* 1994; Krahn *et al.* 1997; Beckmen *et al.* 1999, 2002; Loughlin *et al.* 2002). High levels of these contaminants have been implicated with reproductive impairment (Addison 1989), premature births (DeLong *et al.* 1973; Gilmartin *et al.* 1976; Martin *et al.* 1976), birth defects (Arndt 1973), skeletal deformities (Bergman *et al.* 1992), suppression of the immune response (de Swart *et al.* 1994; Ross *et al.*

1995; Ross *et al.* 1996) and disruption of endocrine function (Brouwer *et al.* 1989). Nursing pups tend to be particularly susceptible since high doses of fat-soluble contaminants may be transferred through their mothers' milk. Such contaminants are now ubiquitous in wildlife (Risebrough 1978), making it difficult to establish cause-and-effect relationships.

Pinnipeds can also be impacted by major oil spills or the chronic discharge of oil. Unlike seals and sea lions, fur seals lack thick layers of insulative blubber, and instead rely on air trapped in their dense underfur to keep warm. Oil that comes in contact with fur diminishes insulating capacity causing some animals to become hypothermic and die (St. Aubin 1990). Oil can also irritate mucous membranes, cause inflammation of skin, or induce other deleterious effects if ingested or inhaled (St. Aubin 1990). An oil spill near a rookery during the breeding season, or when animals are concentrated during the migration (e.g. Unimak Pass in December) could have major impacts (French *et al.*, 1989; Neff, 1990). Impacts of an oil spill in British Columbia would likely be less destructive than near summer breeding grounds. There is no evidence fur seals were impacted by the Exxon Valdez oil spill (Loughlin 1994). Nevertheless, oil discharge from tankers traversing the coast is a chronic problem affecting seabirds and likely northern fur seals as well, but it occurs too far offshore to recover oiled carcasses (Willis and Trites 2006).

Since direct human-induced mortality does not appear to be causing the decline of the Pribilof Island stock, hypotheses to explain it have focused on bottom-up or top-down ecological forcing mechanisms, such as nutritional stress resulting from reduced abundance or availability of prey resources, or increased predation levels or shift in diet of killer whales (*e.g.* Trites 1992). The decline of northern fur seals coincided with declines in Steller sea lions, harbour seals and other apex predators in the Bering Sea and Gulf of Alaska, suggesting some common element may be involved (Merrick 1997; Trites *et al.* 1999; Springer *et al.* 2003; DeMaster *et al.* 2006; Wade *et al.* in press). Changes in prey availability can be caused by natural or anthropogenic factors, such as changes in ocean climate, over-fishing, or natural cycles or regime shifts (Anderson and Piatt 1999; Burton and Koch 1999; Hirons *et al.* 2001; Benson and Trites 2002; Hunt Jr. *et al.* 2002; Trites *et al.* 2007). Its particularly important that prey be available within commuting distance of rookeries when females are lactating (Gentry 1998). The acute effects of reduced prey availability are evident from the abrupt declines in fur seal pup production on San Miguel Island during *El Nino* events (Figure 2f) (DeLong and Antonelis 1991; Melin and DeLong 1994; Melin *et al.* 1996; Melin and DeLong 2000). At more northerly latitudes, longer-term fluctuations or oceanographic regime shifts may have influenced northern fur seal prey, specifically early life-stage forage fish (Sinclair *et al.* 1994; Beamish and Bouillon 1993; Sinclair *et al.* 1996; Anderson *et al.*1997; McFarlane *et al.* 2000; Benson and Trites 2002). Changes in fur seal diets have been noted, with some prey such as capelin disappearing and others like pollock assuming a more prominent role (Sinclair *et al.* 1994, Sinclair *et al.* 1996, Antonelis *et al.* 1997). The fishing effort that was relocated to protect critical habitat of *endangered* Steller sea lions has shifted to important foraging areas for northern fur seals (Robson *et al.* 2004; Robson and Fritz, cited in NMFS 2006).

Fowler (1986) concluded that, given the data and analyses that were available, it was not possible to clearly determine whether the Pribilof fur seal population was currently at, above, or below carrying capacity; whether carrying capacity had changed significantly in the last two or three decades; or whether the observed population decline was due to declining carrying capacity, increasing human-induced mortality, or some combination of these factors.

2. POPULATION DYNAMICS – ST. PAUL ISLAND

St. Paul Island represents the largest and most intensively studied northern fur seal rookery, and the origin of most animals wintering in the northeastern Pacific Ocean. Because fur seals segregate by sex and age during their migration, information on the sex- and age-structure of the total population is required to estimate the abundance of fur seals wintering along the west coast of North America and in British Columbia.

Population projection models have been developed and used in previous studies to assess how the St. Paul fur seal stock was impacted by the female kills during the herd reduction program and pelagic collections, and to assess the sensitivity of the population to changes in juvenile and adult survival and reproductive rates (York and Hartey 1981; Trites 1984[2]; Trites and Larkin 1989; Eberhardt 1990; Smith and Polachek 1981; see reviews by York 1987 and Ragen and Fowler 1992). In this Section, I use projection models to investigate more recent changes in sex- and age-structure that would be expected following the termination of the subadult male harvests. Previous models were driven largely by year-to-year changes in juvenile survival rates (Lander 1979; York 1995) and the number of animals removed during the herd reduction program, scientific collections and subadult male harvests (York and Hartley 1981; Trites and Larkin 1989). However, because the commercial harvests have been terminated and samples are no longer available, annual changes in juvenile survival can not be estimated beyond 1980. There was also evidence of temporal changes in reproductive rates in the pelagic samples collected during 1958-74 (Trites and York 1993), but again more recent samples are no available. Given the lack of recent data, I instead ran a series of simulations to assess the magnitude of changes in key vital rates (juvenile survival, adult survival, and pregnancy rate) that would be necessary to cause the observed declines in pup production, and to assess the corresponding changes in sex- and age-structure of the population.

2.1 Projection Model

The model was based on the numerical models developed by York and Hartley (1981) and Trites and Larkin (1989) to project population changes in annual increments. The population was structured by sex, s (f=female and m=male), and age x in years (0 to 25 years for females and 0 to 16 years for males), with the number of animals of sex s and age x at time t denoted by $N_{s(x)t}$. The number of animals surviving to the next year, t+1, by which time they aged x+1, was estimated as:

$$[1] \quad N_{s(x+1)t+1} = N_{s(x)t} \cdot SV_{s(x)}$$

where $SV_{s(x)}$ represents the finite annual survival rate of animals of sex s from age x to age x+1. The expected number of pups recruited to the population, which is assumed to occur as a pulse during the breeding season, was estimated from the proportion of females aged x that were pregnant, $PR_{(x)}$:

$$[2] \qquad N_{s(0)t} = \sum PR_{(x)} \cdot N_{f(x)} \qquad \text{for } x = 1 \text{ to } 26$$

The projections were calculated in an Excel spreadsheet, but are computationally equivalent to classic matrix models (Lewis 1942; Leslie 1945). Comparison of the predicted number of pups born with counts of live and dead pups made at the end of the birth season provided a measure of the goodness of fit of the projections.

For the base model, it was assumed that survival rates of animals aged >2 years and reproductive rates were constant over time. For females, I used the survival schedule given in Table 3 in York and Hartley (1981) and Lander (1981), which they obtained by fitting (and extrapolating) a Gompertz equation to the age frequency distribution of the pelagic specimens collected during 1958-74. For males, I used the natural survival rates used by Lander (1981) for St. Paul Island based on Chapman's (1964) inferred survival of males aged 6-10 years, and Johnson's (1968) age-composition data for older bulls. For juvenile male survival to 2 years of age, I used Trites' (1984, 1989) Type I estimates, which were a refinement of Lander's (1975) original estimates using somewhat more realistic assumptions. Some of the early models assumed that females experienced survival rates 1.05 – 1.10 times higher than males (Chapman 1964), but more recently Trites (1984), Trites and Larkin (1989) and Eberhardt (1990) concluded there was no evidence of differential survival rates between sexes, so I applied the male estimates to both sexes. Annual estimates of juvenile survival could not be calculated beyond 1980 due to termination of the male harvest so, following Trites (1984), I applied the average juvenile survival rate observed over the last decade data were available. York and Hartley (1981) assumed an equal sex ratio at birth, whereas Trites (1984, 1989) assumed a sex ratio 0.51:0.49 in favor of females. However, based on the cumulative data summarized in Antonelis *et al.* (1997) and Fowler (1998), I assumed a slightly skewed sex ratio of 0.50:0.5065 favoring males.

Prior to running the simulations, I ran a series of preliminary projections to iteratively determine the equilibrium juvenile survival rate that would result in stationarity (a stable sex- and age-structure with no population growth), and simulations were subsequently initiated in 1950 using a stationary sex- and age-structure. During the female herd reduction and pelagic collections, I removed female kills just prior to the breeding season based on the age structure of reported kill (i.e. this implies any pups born before mothers were killed would have died). The number and age-composition of females killed on St. Paul Island were taken from Table 1 in York and Hartley (1981), and the sex- and age-composition of pelagic kills tabulated from the NPFSC pelagic database, which resulted in values almost identical to those given in Table 2 in York and Hartley (1981). As per York and Hartley (1981), I assumed 80% of the pelagic kills were from the St. Paul Island rookery. For ages that were unknown or reported as 7+, 8+ or 10+ (1%, 5%, 11% and 2% of the total female kill respectively), I amortized the kills among ages over the plausible age range based on the relative distribution of known-aged kills over the same age range in the entire sample.

York and Hartley (1981) focused on the female segment of the population, whereas Trites (1984) and Trites and Larkin (1989) also included male projections. Males were more problematic in that the only reference by which to evaluate the projections are the time-series of harem and idle bull counts. While these older (approximately age 7+ years) males are distinctive and have been counted in a consistent manner, they represent only an index of abundance. Unlike pups, males are not necessarily confined to land, and it is not known what fraction of males are present on land or their age composition, and how the age-composition or proportion hauled out may have changed with population status or its sex- and age-structure. Moreover, the territorial bulls represent a small remnant of cohorts born roughly a decade earlier, and during the intense commercial male harvests the vast majority of males were killed at 2-5 years of age. The projections could not be initiated prior to 1950, due to uncertainly regarding pup production during the 1940s (York 2005a) and uncertainty regarding the age-composition of male harvest prior to the development of ageing techniques in 1950. Consequently, the projections for the first decade or so are almost entirely a function of the assumptions made about the initial age distribution and age composition of the harvest, so I only considered the projections to be meaningful starting in the early 1960s[3].

Harvest rates of subadult males in the 1950s and 60s were high. The goal was to maximize the number of skins harvested, leaving only sufficient number of males required for breeding in a highly polygamous mating system. In several cases, the estimated number of males taken from an age-class slightly exceeded the estimated number of animals within the age-class. I thus constrained the kill to 95% of any year-class to prevent negative numbers. For a few years after 1984 where I didn't have access to complete statistics on annual subsistence takes, I applied the averages kill and age-composition in the preceding and proceeding years. Since the subsistence kills were about two orders-of-magnitude lower than the commercial harvests, these uncertainties had a negligible effect on the projections. I attempted to assess the fit of the male projections by comparing the projected number of older males with harem and idle bull counts.

From an ecological perspective, biomass may be a more relevant metric of population size, especially where there is a large disparity in mass of females and males, and where there has been a pronounced demographic shift in sex- and age-structure. Following Lander (1981), I estimated the mean mass of males and females in the population, $\overline{BM}_s$, based on the sex- and age-composition:

$$[3] \qquad \overline{BM}_s = \sum (N_{s(x)t} \cdot N_{s(x+1)t+1})^{0.5} \cdot BM_{s(x)}$$

where and $BM_{s(x)}$ represents the average body mass by sex and age, and the summation is for x = 0 to 26 years for females and 0 to 16 years for males. Whereas Lander (1981) calculated the biomass at the peak of the breeding season, I was more interested in the average biomass over the entire year. I thus took the geometric mean of the number of animals present at the beginning and end of the year (aged x and $x+1$) as a measure of the average number present during the year, which assumes mortality was uniformly distributed throughout the year. The mean biomass of females was estimated from pelagic data pooled across all months for all years. Body mass was tabulated separately for pregnant and non-pregnant animals, and subsequently weighted according to age-specific pregnancy rates (Table 3 in York and Hartley 1981). For males, I adjusted the biomass estimates given by Lander (1981), which were similar to the values reported by Gentry (1998). In both cases, the body masses of older males had been obtained from territorial bulls at the beginning of the breeding season when they were likely in peak condition. Gentry (1998) indicated males lost an average of 32% of body mass during the breeding season, at which point they were probably in their poorest condition. Lander's (1981) body masses for males age 7+ years were therefore reduced by 16% to estimate the average biomass of males throughout the year.

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[3] I explored initiating the male projections in the 1940s based on extrapolated or interpolated pup counts and using a typical age-composition for the harvest, but results varied widely depending on these subjective assumptions. Trites (1984) presented male projections starting in 1950, but I would argue they were almost entirely an artifact of the assumptions he made about the initial age-composition, which might explain why they did not track the observed bull counts until the 1960s.

2.2 Population Dynamics

For females, the projection models used by York and Hartley (1981) and Trites and Larkin (1989), and my hybrid of their models, all fit the pup counts fairly well during the period of herd reduction program (Figure 3). The models indicated that about 70% of the decline in pup production was directly attributable to the removal of females during the herd reduction and pelagic collections. York and Hartley (1981) subsequently predicted a slight increase in the 1970s and early 80s, whereas the Trites and Larkin (1989) predicted a period of stability. Although the models used slightly different survival and reproductive schedules, the primary reason for the difference was York and Hartley (1981) assumed juvenile female survival was higher than the measured rates for males, whereas Trites and Larkin (1989) applied the measured male rates to both sexes. Both models indicated that about 30% of the decline could not be accounted for by the female kill, and was due to variability in juvenile survival, particularly the poor survival during 1952-57 and to lesser extent during 1972-76. In years of abnormally high juvenile mortality, the initial size of cohorts recruited to the population was reduced, resulting in a decline in pup production several years later as that cohort attained breeding age. Overall, during 1950-82, juvenile survival to age 2 years averaged 0.373, which was about 94% of the equilibrium value of 0.397.

Projections beyond 1980 were hindered by the lack of information on annual changes in juvenile survival. Trites and Larkin (1989) made projections beyond 1980s using the average survival rate of 0.325 that had been observed over the last decade data were available (1971-80). The reduced juvenile survival explained a large part of the decline in pup production during the early 1980s. Extending those projections with my hybrid model using the same juvenile survival rate, they appear to track the average decline of 2% per annum in observed pup counts (Figure 3). Thus, one plausible explanation for the recent declines in pup counts is that juvenile survival has remained below equilibrium levels since the early 1970s. A 2% rate of decline in pup production could also be obtained by applying the equilibrium juvenile survival rates and decreasing adult survival (aged 2+ years) to 98.1% of base values, or reducing pregnancy rates to 88% of base values (Table 5). The necessary changes are all biologically realistic and within the range of inter-annual variability observed for each parameter when data were available (Smith and Polacheck 1981; Trites and York 1993). Trites and York (1993) found that pregnancy rates of females aged 8-13 wintering in coastal waters between California and British Columbia declined from roughly 0.90 to 0.78 during 1958-72, compared with an average of 0.873 for all years combined. The mean age at which females gave birth to their first pup also decreased (Trites and York 1993), and could have contributed to density-dependent changes in reproductive rates, but the model is relatively insensitive to such changes (Olesiuk, unpublished data). In reality, the there were likely concurrent changes in several of the vital rates, its unlikely they were occurred uniformly over all ages, and probably fluctuated over time (Smith and Polacheck 1981). Its also likely that dispersal of reproductive females to other breeding sites have contributed to the declines in pup production on St. Paul Island. For example, the explosive growth in pup production at Bogoslof Island over the last decade (1996-2006) equates to about 20% of the decline on the Pribilof Islands over the same period. Given the larger size of the Pribilof Island stock compared to other rookeries, a 2% rate of emigration would represent an immigration rate of 3% to other rookeries, which would be difficult to discern given the lack of recent tagging and resighting effort.

Although it remains uncertain as to what is driving the decline in pup production (and certainly no information on causes for the year-to-year variations), the model indicates the magnitude of changes in key vital rates required were rather modest, and none would have had a major impact on the pup multiplier, overall sex- and age-composition, or mean body mass of females. Regardless of the which parameter is varied, females pup multipliers vary from 4.8 to 5.9 (±11% of the mean) over the last 30 year projection (Figure 5a), with the lowest values corresponding with reduced juvenile survival rates and the highest values with reduced pregnancy rates[4]. The predicted values are similar to Lander's (1981) multiplier of 5.2 for a harvested population, and Loughlin *et al.*'s (1994) adjusted value of 5.9 for an unexploited population. The mean body mass of females was estimated to range from 22.9 to 24.8 kg. (Figure 6a). Thus, even without specific knowledge of the nature of changes in vital rates, its possible to make reasonable inferences about the total abundance, age-composition, and biomass of the female component of the population.

Projection of the male component of the population proved more problematic and the results are more speculative. As noted above, the projections were initiated in 1950, but the results were not considered meaningful until the early 1960s, by which time unknown-sized cohorts recruited in the 1940s had propagated through the bull population. The management goal during the male harvest was to remove surplus males, leaving just enough required for breeding. According to York (2005a), early investigators like Osgood (1915 cited in York 2005a) and Kenyon *et al.* (1954) tacitly assumed that all adult males (aged about 7+ years) were on land during the breeding season, such that the counts of territorial males actually reflected total abundance, rather than merely an index of relative abundance. The projections for the 1960s and 1970s seem to support this, as the projected number of males aged 7+ years in the population appears to track the total harem and idle bull counts (Figure 4). Indeed, at their lowest levels, the projections indicate there would have been too few 7+ males in the population, and perhaps some 6+ males were included in the bull counts. A second decline in bull counts occurred in the 1980s (Figure 4), which was attributable to the sharp decline in pup production that had occurred a decade earlier (Figure 3). The reason for the sharp decline in pup production in the late 1970s is unknown, as annual estimates of juvenile survival rates were no longer available. Trites and Larkin (1989) suggested that the abruptness of the decline indicated a sudden drop in adult female survival rates, although pup production appears to have subsequently stabilized during the 1980s (Figure 3).

As expected, there was a dramatic increase in the number of territorial bulls in the late 1980s as the unexploited male cohorts attained breeding age. However, the magnitude of the observed increase in bull counts was much less than the number of older males estimated to have survived. Indeed, by the turn of the century its estimated there were only half as many territorial bulls counted on beaches than 7+ males in the population (Figure 4). The reason for this large discrepancy is unknown. There could be a density-dependent or social aspect to the proportion of bulls that take up territories, such that a smaller proportion are on beaches when male densities are high. Its also possible males spend more time foraging at sea, or may not return to the Pribilof Islands, when beaches are already occupied. Its also possible the age-composition of bulls has changed with male densities – the increase in bull counts in the 1970s that resulted from the increase in pup production in the 1960s, seems to track the timing and number of males aged 6+ years. However, the more recent increase in bull counts in the 1990s that resulted from the cessation of the harvest seems to track the timing and number of males aged 9+ or 10+ years. Johnson (1968) indicated that bulls were not fully recruited to breeding population until 10 years of age, whereas others have assumed all males aged 7+ are counted (see review in York 2005a). Perhaps there is some upper limit to the ratio of territorial males to reproductive females, as the

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[4] This argument assumes there have not been counteracting changes in vital rates. If, for example, pregnancy rates actually increased, but were offset by even lower survival rates, there could be a broader spectrum of population conditions that would result in a 2% decline in pup production.

recent declines in bull counts seem to parallel the declines in pup production (whereas the number of 7+ males estimated to be in the population is at very high levels). The only other explanation would seem to be there has been a dramatic increase in the mortality or dispersal rate of males during the last few years. I am not familiar enough with the counts and biology of the species to assess these possibilities.

Assuming the male projections are reasonably accurate, termination of the male harvest resulted in a dramatic shift in the age distribution of males in the population. The model projected that due to the increased prevalence of males - not only territorial males, but also subadult and young adult animals - the ratio of male pups to total males multiplier increased from a low of just under 2.0 in the late 1970s to a high of just over 3.0 in recent years (Figure 6b). Loughlin *et al.* (1994) adjusted life table also implies a 5-fold increase in prevalence of males aged 5+ years. Corresponding with the shift from a harvested to unexploited state, mean body mass of males is was also estimated to have increased substantially, from a low of 14 kg (i.e. a male population highly skewed toward pups, yearlings and 2-year olds) to a high of 38 kg in recent years (i.e. a male population with a natural age-structure) (Figure 6b). As a result of their increased abundance and larger mean mass, the contribution of males to total population biomass was estimated to have increased from 20% in the mid-1970s to 49% in recent years (Figure 6c).

3. MIGRATION – WEST COAST NORTH AMERICA

3.1 General Migration Patterns

Northern fur seals do not breed in Canada, but distribute widely during their pelagic migration, and the waters off British Columbia constitute an important wintering area. The migration is complex, with movement patterns differing between sexes and varying with age, such that the population becomes segregated by sex and age. The following qualitative account of migration patterns in the eastern Pacific Ocean, with particular attention to British Columbia, is synthesized from historic sealing records, pelagic collections and sightings during research trips, and incidental sightings from platforms-of-opportunity (Townsend 1899; Kenyon and Wilke 1953; Pike *et al.* 1959; Manzer *et al.* 1969; Murie 1981; Bigg 1986, 1990), with additional insight provided by VHF and satellite telemetry (Loughlin *et al.* 1993, 1999; Ragen *et al.* 1995; Ream *et al.* 2005).

The migration begins when animals leave the Pribilof Islands between September and November. Pups generally depart in late October or November, by which time most other animals have already dispersed. VHF tracking indicates pups tend to travel south and within a few week enter the North Pacific Ocean through passes such as Unimak Pass (Ragen *et al.* 1995). Young animals spread out across the ocean and become widely distributed on the high seas (Townsend 1899; Manzer *et al.* 1969), with some moving as far south as California by December (Kajimura 1979). Some juveniles enter coastal areas, and occasionally small aggregations of yearlings can be found in the protected inlets along the British Columbia and SE Alaska coast (Pike *et al.* 1959; Bigg 1990). Young animals remain at sea through their first and second years and sometimes third years. These young animals presumably account for most of the offshore observations of animals seen throughout the year (Manzer *et al.* 1969; NMFS 2006). A few animals return to the Pribilof Islands in August at 2 years of age, but judging from age-composition of the male harvests most do not return until 3 or 4 or perhaps even 5 years of age (males aged 2, 3, 4 and 5 years account for 0.1%, 5.0%, 59.5%, and 32.5% of the male harvest during 1950-1983; Lander 1980a; Trites and Larkin 1989).

Adult males leave the Pribilof Islands in October, and tend to winter at northerly latitudes in the southern Bering Sea, Sea of Okhotsk, and northern Gulf of Alaska (Townsend 1899; Kenyon and Wilke 1953; Bigg 1990). Loughlin *et al.* (1999) tracked 8 adult males from the Pribilof Islands to wintering areas in the Gulf of Alaska or the western Pacific Ocean off the Kurile Islands or Japan. Densities of older males increase in the Gulf of Alaska in April-May as they make their way back to the Pribilof Islands (Bigg 1990), where they arrive in late May and June (Bigg 1986).

Adult females tend to leave the Pribilof Islands in October-November, and pass from the Bering Sea into the North Pacific in late November and early January (Ream *et al.* 2005). They tend to migrate across the open ocean to more southerly latitudes (Ognev 1935; Manzer *et al.* 1969; Bigg 1990; Ream *et al.* 2005), although a few may spend some time in the Gulf of Alaska before heading south (Ream *et al.* 2005). The densest wintering concentrations occur in coastal areas over the continental shelf and along the shelf break, where they begin arriving between December and January (Townsend 1899; Bigg 1990; Antonelis and Perez 1984). The transition zone also appears to be an important foraging area for older females (Ream *et al.* 2005), and may serve as a southern barrier for fur seals and their prey (Sinclair, 1990; Beamish *et al.*, 1999; Ream *et al.*, 2005). Pregnant females arrive in coastal wintering areas in January and depart in March-May. Most pregnant animals reach western Alaska by June and arrive on the Pribilof Islands during July, where they give birth and nurse pups until October-November (Peterson 1968; Gentry and Holt 1986). Non-pregnant females depart wintering areas and arrive on the Pribilof Islands in August and September, about a month later than pregnant females (Bigg 1986). Ream *et al.* (2005) tracked 2 adult females through their entire migration, and estimated the total distance traveled to be 9,272 and 9,732 km over a period of 244 and 233 days respectively. Including the pelagic migration and foraging trips while lactating, females spend all but about 35 days at sea (Gentry 2002).

Females from rookeries in the Bering Sea tend to winter along the west coast of North America, and females from Russian rookeries tend to winter along the Asian coast. There is, however, considerable mixing of stocks during the migration (Baba *et al.* 2000). Taylor *et al.* (1955) estimated that about 5% of females from the Pribilof Islands wintered on the Asian coast, and because the western population was much smaller at the time, the eastern animals constituted 27% of females aged 3-5 years wintering off Japan. However, more complete analysis of tags recovered off eastern Japan indicate that 63% of 342 tag recoveries were from Robben Island, 30% from the Commander Islands, 6% from the Pribilof Islands, and 3% from the Kurile Islands (NPFSC 1975). Animals tagged as pups and subsequently recovered off the west coast of North America indicate 96% originated from the Pribilof Islands, 4% from the Commander Islands, and less than 1% from Robben Island (Lander and Kajimura 1982; DeLong 1982). Of the 225 tagged seals collected off British Columbia and Washington (the areas overlapped for tag recovery information), 78% had been born on St. Paul Island and 19% on St. George Island in the Pribilof Islands, and 2% on Medney Island and 2% on Bering Island in the Commander Islands (Perez 1997). While these tag recoveries indicate that exchange of eastern and western animals occurs, they do not accurately reflect true dispersal rates because far greater numbers of tags were deployed on the Pribilof Islands as part of pup production estimates (York 2005a), no seals have been tagged on the Kurile Islands, and pelagic sampling ended when the San Miguel was still very small and before the Bogoslof Island rookery had become established.

No information has been published on the migration patterns of fur seals from Bogoslof Island, but given its proximity to the Pribilof Islands (165nm SSE of St. George Island), and since most of the animals are presumed to have emigrated from the Pribilof Islands, I assumed they followed the same migration pattern as Pribilof Island animals (and thus constitute about 8% of the animals wintering off the west coast of North America). In contrast, the San Miguel stock is apparently less migratory, with the vast majority of animals remaining off California throughout the year (Antonelis and Perez 1984), so I assumed none occurred in Canadian waters. The latter assumption had little effect on the abundance estimates, since the San Miguel stock is only about 1% the size of the Pribilof Island stock.

3.2 Sex- and Age-Composition and Abundance

A total of 10,743 fur seal specimens of known sex and age were collected in coastal waters along the west coast of North America (WCNA, herein defined as waters within 200 km of shore between California and Cape Suckling, Alaska). The majority (72%) were females aged 3+ years, with yearlings being the second most prevalent age-class (12%). Figure 7 shows the sex- and age-composition of the pelagic specimens collected compared to the predicted sex- and age-structure of the population between 1958-74 (Section 2.2). Young animals of both sexes were under-represented in the pelagic collections. The relative proportion of females increased with age, such that the age distribution of older females resembled the expected age structure of the population[5], leading previous investigators to assume females were fully recruited to coastal areas by about 8 years of age (Lander 1981; York and Hartley 1981; Bigg 1990). However, more recent satellite tracks indicate that some old females can winter offshore (Ream *et al.* 2005). Of the 10 adult females tracked to wintering areas, 8 were judged to have been 8+ years of age, and 6 of those wintering in coastal areas and 2 along the transition zone (R. Ream, NMML, pers. comm.). I therefore assumed that 75% of females aged 8+ were represented in the coastal collection, and estimated the proportion of younger age-classes represented in coastal areas based on their relative abundance compared with the 8+ females. Except for yearlings, males were uncommon in the pelagic collections, indicating few wintered in coastal areas at southerly latitudes. Overall, it was estimated that 27% of yearlings (56% female), 40% of juveniles aged 1.5-3.5 years (78% female), 74% of females aged 4.5+ years, and 9% of males aged 4.5+ years wintered along the WCNA, representing 52% of the total population. These values are similar to the figures used by Antonelis and Perez (1984) who, based on their familiarity with the pelagic data and population dynamics of fur seals, assumed that 80% of females aged 5+ years, 30% of immature seals, and 10% of adult males wintered in coastal waters off the continental U.S. It thus appears that segregation by sex begins in the first year and is well developed prior to adulthood. It should be noted that there was likely some sampling bias in the pelagic collections, with yearlings being more susceptible to hunting and over-represented because small aggregations were sometimes encountered in protected areas, and adult males under-represented because they were not as easily killed with shotguns as smaller animals. However, these two age-groups constituted a fairly small component of the total number of animals collected (11.8% and <0.1% respectively), so the bias would have to be large to affect the overall abundance estimate.

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[5] The similarity of the age-structure of females in the pelagic collection and projected by population model is not coincidental, as the projected values are a function of the survival rates used in the mode, which were estimated using the pelagic collection data. The key assumption is that the relative proportion of females wintering in coastal areas does not change beyond about 8+ years, and that the absolute proportion of females wintering in coastal areas as opposed to offshore was accurately reflected by satellite tracks for females aged 8+ years (Ream *et al.* (2005), and R. Ream, NMML, Seattle, personnel communication).

Based on the proportion of each sex- and age-class wintering along the WCNA, and the sex- and age-composition and size of the Pribilof and Bogoslof Island fur seal stocks, its estimated that roughly 367,0000 migrants would be wintering in coastal waters off the west coast of North America when fur seals are at peak seasonal abundance in April. An additional 8,600 non-migrants from San Miguel Island would occur off California.

3.3 Seasonal Distribution

The pelagic sealers were quite familiar with the general movements of fur seals and the high densities that wintered in coastal areas (Townsend 1899; Murie 1981). Victoria on Vancouver Island was the a major centre of sealing during 1882-1911, and detailed logbooks were maintained on the number and date fur seals were taken. Seals were hunted from canoes and skiffs launched from sailing schooners, the position of which was recorded daily, providing a record of the general location of kills. The schooners traveled widely, making either year-long trips across the Pacific, spring trips along the west coast, or summer trips to the Bering Sea (Murie 1981). Data from logbooks for the eastern Pacific have been tabulated and summarized by Murie (1981), representing kill records for a total of 258,120 seals. The logbooks provide information on seasonal occurrence and movements along the west coast, but no data on age or pregnancy status, and the information on sex is not deemed reliable (Murie 1981). The sealing records show how the fleet followed seals, taking them wherever there were sufficient densities (hunting was not permitted within 60 nautical miles of the rookeries) (Figure 8). Along the west coast of North America, there was northward shift in harvests over the wintering period (Figure 9 and 10). Sealing began off California in December, peaked in February, and few were taken after March. Sealing off Oregon and Washington did not begin until February, and peaked in March, with few taken after April. Sealing off British Columbia began in March and peaked in April, with few taken by May. Off SE Alaska, most seals were taken in April. Few seals were taken in coastal areas by May, suggesting they (or the sealing fleet) had started their trek across the ocean towards the Bering Sea.

A second source of information on migration patterns is the fur seal sightings made by Canada and U.S. vessels during pelagic research collections in 1958-74 as part of the North Pacific Fur Seal Commission research program (Figure 11). A total of 14,600 hours of dedicated sighting effort was conducted during research trips along WCNA, during which 37,221 seals were sighted (mean of 2.4 seals per hour). A total of 15,550 specimens were also collected along WCNA, which provided complimentary information on sex- and age-composition, reproductive status, and diet in each region by month. Following Antonelis and Perez (1984), I estimated the relative numbers of seals in each region by month (for all years combined) based on the average sighting density multiplied by the size of each region. The regions used corresponded with those delineated by the North Pacific Fur Sea Commission with two exceptions. For British Columbia, the NPFSC border had been drawn at 49ºN, such that LaPerouse Bank, an important wintering area, was included with Washington State. I realigned the border to correspond with the political boundary, so as to obtain a more accurate estimate of the relative abundance in Canadian waters. Since I was interested in the northward migration along the mainland coast, I created a SE Alaska region that was a subset of Gulf of Alaska but included only waters east of Cape Suckling (144ºW).

The NPFSC sighting data provide a similar picture of the migration pattern as the sealing records (Figures 12 and 13), suggesting the general pattern had remained fairly constant over the half century (including a period of severe depletion) that lapsed between the collection of the two datasets. Fur seals began to appear in coastal areas in December and increased abruptly in January (Figure 13). Overall densities were relatively stable from February to May but, as indicated by the sealing records, the highest densities shifted northward over the winter from California in February, Oregon and Washington in April, and British Columbia and SE Alaska in May (Figures 12 and 13). Numbers declined abruptly in June, with no seals seen by July. Integrating the area under the sighting curve (Figure 13), and dividing by the estimate of peak abundance (Section 3.2), mean residency period in coastal waters was estimated to be about 4.8 months.

In British Columbia, seals began to appear in December and were present until June. Abundance peaked in May, at which point about 34% of the total WCNA population, or roughly 123,000 fur seals, were wintering in Canadian waters. Mean residency in Canadian waters was estimated to be 3.1 months. During the seasonal peak, fur seals were the most abundant pinniped on the west coast of Canada, being about as numerous as all other species combined (Table 4). The main wintering concentration occurred on La Perouse Bank off SW Vancouver Island (Figure 14), which accounted for about 81% of the specimens collected during 1958-74 and 52% of the pelts harvested during 1891-1911. Based on the pelagic research samples, 55% of the animals collected in this area were adult females, most of which were pregnant. Lower densities occurred off NW Vancouver Island, in Hecate Strait and up inlets, which were mainly yearlings and juveniles.

3.4 Diet

Northern fur seals are opportunistic predators and their diet changes depending on the local and seasonal availability of suitable prey species. Detailed descriptions of diet and foraging habits have been provided by numerous authors (e.g. Kajimura 1984; Perez and Bigg 1986; Perez and Mooney 1986; Antonelis and Perez 1984). NMFS (2006) provides a summary of current information on the feeding habits of fur seals in the Bering Sea and Gulf of Alaska. A comprehensive analysis of feeding habits was beyond the scope of this assessment, and my goal was to merely identify the key prey species utilized by fur seals during their winter migration along the west coast of North America, particularly off British Columbia.

A total of 10,743 fur seal specimens were collected along the WCNA during the pelagic research collections, and 5,048 (47%) contained non-trace amounts of identifiable prey in their stomachs[6]. Although the overall diet was diverse, with over 70 different prey species having been identified, the diet in any given area at a given time was usually dominated by a few key prey species (Perez and Bigg 1986). Off California, the principle prey were northern anchovy (45% of stomachs), Pacific hake (30%), gonatid/onychotuethid squid (24%), Pacific saury (16%), market squid (9%), jack mackerel (4%) and rockfish (3%), which collectively accounted for 93% of all prey items identified. Off Oregon and Washington, the principle prey were northern anchovy (27%), gonatid/onychotuethid squid (20%), rockfish (18%), salmon (15%), herring (12%), capelin (11%), eulachon (5%), hake (5%), market squid (5%) and American shad (4%), which collectively accounted for 86% of all prey items identified. Off British Columbia, the principle prey were Pacific herring (45%), gonatid/onychotuethid squid (24%), salmon (16%), rockfish (6%), market squid (5%), sablefish (5%), sticklebacks (5%), eulachon (3%), sandlance (3%), hake (2%) and northern anchovy (2%), which collectively accounted for 87% of all prey

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[6] Trace occurrences <5ml, which were often comprised of cephalopod beaks which can persist in stomachs much longer than other prey remains (Bigg and Fawcett 1985), where thus excluded from the analysis.

items identified. Only 13% of the salmonids were identified to species level, and were comprised of 48% pink salmon, 24% coho salmon, 14% chinook salmon, 10% chum salmon, and 5% steelhead; no sockeye salmon were identified. Off SE Alaska, the principle prey were Pacific herring (66%), gonatid/onychotuethid squid (14%), salmon (6%), capelin (4%), and pollock (3%), rockfish (2%), and sandlance (2%), which collectively accounted for 96% of all prey items identified.

3.5 Comparison With Other Pinnipeds

During the most recent decline of northern fur seals on the Pribilof Islands, abundance of Steller sea lions, harbour seals and other apex predators in the Bering Sea and Gulf also declined, suggesting a common factor may have been involved (Merrick 1997; Springer *et al.* 2003; DeMaster *et al.* 2006; Fadely *et al.* 2006; Wade *et al.* in press). In contrast, pinnipeds along the west coast of North America have increased in recent years. California sea lions (*Zalophus californianus*) were decimated by over-hunting in the 19th century, and by 1927 only 1,229 non-pups were found at Santa Barbara, San Clemente, and San Miguel Islands (Bonnot and Ripley 1948). Since that time, censuses at rookeries in the Southern California Bight indicate numbers have been increasing exponentially at an average rate of about 6% per annum, and the population is now estimated to number about 240,000 (Stewart *et al.* 1993; Lowry and Maravilla-Chavez 2005). The eastern population of Steller sea lions, which had also been depleted by hunting and predator control programs, has been increasing at about 3.1% per annum since the last large kills in the mid-1960s, and current abundance is estimated at 48,000-57,000 (Calkins et al. 1999; Olesiuk 2003; Pitcher *et al.* 2007). Harbour seals have also increased in most areas along the west coast of North America since being protected in the early 1970s, although populations may have attained or are approaching carrying capacity (Olesiuk *et al.* 1990; Brown 1997; Olesiuk 1999; Small *et al.* 2003; Jeffries *et al.* 2003)

Gentry (1998, 2002) astutely noted that fur seals and sea lions do not directly compete. Fur seals tend to forage on the continental shelf and shelf break, consuming small forage or juvenile fish, whereas sea lions tend to forage more inshore and their diet includes larger species and adult age-classes. While perhaps not always in directly competition (although there is considerable overlap in distribution; Antonelis et al. 1990; see Figure 9 *vis-à-vis* Lowry and Forney, 2005), the fur seals and sea lions certainly utilize many of the same prey resources. For the most part, the same prey that dominate the diet of fur seals off California, also dominate the diet of California sea lions off California (Figure 15a). Similarly, the diet of fur seals wintering off British Columbia and SE Alaska is strikingly similar to the diet of Steller sea lions in the same region (Figure 15b). Even though there is essentially no spatial overlap in the foraging areas of pelagic fur seals and coastal populations of harbour seals, they nevertheless are dependent on some of the same prey stocks, which themselves are migratory. For example, the high densities of harbour seals in the Strait of Georgia, British Columbia, rarely venture offshore, but feed on migratory prey such as herring and salmon when they move inshore to spawn (Olesiuk 1993). These same herring and salmon stocks are important prey for fur seals, but are taken during the pelagic phase of their life cycle. Indeed, there seems to be nothing unique about the diet and prey requirements of northern fur seal diets that would set them apart from these other pinnipeds, except for the higher prevalence of gonatid/onychotuethid squid, which tend to be taken by fur seals further offshore (Perez and Bigg 1986) beyond the foraging range of sea lions and harbour seals.

Given the disparity in body-size between fur seals and the two species of sea lions, comparison of these apex predators is probably more meaningful in terms of biomass than numerical abundance. I thus calculated the biomass of California and Steller sea lions using life tables (Calkins and Pitcher 1982; Lowry and Maravilla-Chavez 2005; Pitcher *et al.* 2007) and growth curves (Belda 1970; Calkins and Pitcher 1982; Winship *et al.* 2001) as per Equation 3 (see Section 2.2; Olesiuk, unpublished data). In the 1960s, northern fur seals were the dominant pinniped along the west coast of North America, comprising perhaps 3-times the combined biomass of the two species of sea lions (Figure 16). However, with the decline of fur seals, and recovery of sea lion populations, there has been a dramatic shift in their importance. The biomass of fur seals along the WCNA, which has fallen by half, is now only about one-third the combined biomass of the two species of sea lions (Figure 16).

DISCUSSION

The COSEWIC guidelines for assessing risk of extinction were developed largely on the basis of IUCN criteria, which define a population as a genetically distinct taxon, and subpopulations as units with little demographic or genetic exchange (typically one successful migrant individual or gamete per year or less). SARA legislation also allows for listing of subspecies, varieties, and "geographically or genetically distinct" units, and COSEWIC has defined the latter as cases where "*dispersal of individuals between separated regions has been severely limited for an extended period of time and is not likely in the foreseeable future*" and "*occupation of differing eco-geographic regions that are relevant to the species and reflect historical or genetic distinction*". Only one species and no subspecies or varieties of fur seals are currently recognized (Rice 1998), and there appear to be no discernible genetic differences of animals between breeding sites (Ream 2002). While fur seals in the North Pacific Ocean certainly do not comprise a panmictic population, the degree of exchange of both males and females among breeding sites, the dispersal of reproductive animals to new rookeries, and degree of inter-mixing during pelagic migrations would seem to preclude designation of subpopulations. It is thus concluded that the appropriate scale for assessing the status of northern fur seals is the population level.

Pup production estimates indicate that population trajectories vary among breeding sites. The Pribilof Island stock, by far the largest, is the only rookery that has exhibited prolonged declines, which have continued for about 50 years. The other two large rookeries on the Commander Islands and Robben Island have exhibited little net change in pup production over the last 30 years (3 generations) – and prior to that one had been increasing and the other decreasing. The rookery on the Kuril Islands has exhibited fairly steady growth over the last 50 years, and the new rookery on Bogoslof Island has exhibited explosive growth since it was formed in the 1980s. Given the broad range of population trajectories, its difficult to extrapolate future trends.

Overall, pup production is estimated to have declined by about 38% over the last 30 years (3 generations). During the same period, there has also been a demographic shift in make-up of the population due to termination of subadult male harvests in the 1970s and 1980s, which resulted in a shift from a population skewed toward females and containing few older males, to one with a more natural sex- and age-composition. As a result, total abundance of fur seals is estimated to have declined by 27%, and the number of mature individuals in the population is estimated to have declined by 23%. Interestingly, due to the increased prevalence of adult males, which are larger than females, the decrease in abundance as been offset by an increase in the mean body mass of animals, such that the total biomass of northern fur seals may not have changed much over the last 30 years.

There are two principle sources of uncertainty associated with the abundance estimates: 1) imprecision and bias in the pup production estimates (York and Kozloff 1987; York 2005a); and 2) imprecision and bias in the multipliers used to extrapolate total population size and structure (York 2005b). With respect to pup production, I presented and assessed the estimates without much regard to potential sources of error. In reality, pup production has been estimated using a variety of techniques, the methods have differed among sites and varied over time, and each method has its own set of underlying assumptions and inherent biases (see review in York 2005b). I did not include counts that were projected from expected or theoretical growth rates, or extrapolated from other components of population (e.g. pup numbers extrapolated from the number of females on the rookery). For the most part, the pup estimates were from direct counts made from land, with in some cases non-pups having been driven off rookeries. The exception was the Pribilof Islands where, owing to its size, direct counts were not feasible, and pups numbers were estimated using mark-recapture techniques. While there may be considerable biases associated with these estimates (York 2005a), its unlikely they would affect the general conclusions. There is little doubt that pup production on the Pribilof Islands has declined significantly. Similarly, its unlikely that counting errors would change the general conclusion that there has been little net change in pup production on the Commander Island and Robben Island rookeries over the last 30 years. Finally, there is little doubt there have been significant increases in pup production on the Kuril Islands and Bogoslof Island rookeries.

With respect to the multipliers for estimating total population size, and the sex- and age-structure, there is a wealth of information available on the life history of northern fur seals, especially for females (see Literature Cited). Regarding population dynamics, *Callorhinus ursinus* is probably the most-studied of the fur seals (Wickens and York 1997). As with most marine mammals, there are potential sampling biases associated with the estimates of vital rates, but for northern fur seals the large samples sizes available for females from pelagic collections are unprecedented, and provide estimates of age at first birth, pregnancy rates, survival rates, and growth rates, at least for older females. Moreover, a time-series of annual juvenile survival rates has also been derived based on the subadult male harvests, which for other species often have to be inferred by balancing life tables. For northern fur seals, population models can be independently evaluated by comparing predicted pup production with the actual pup counts. The models developed by York and Hartley (1981) and Trites and Larkin (1989) track the general trends in observed pup counts quite well, and demonstrate a fairly good understanding of the population dynamics of females. The lack of more recent samples to update life history parameters limits our understanding of the current population dynamics, but the simulations presented in this assessment indicate that relatively small changes in vital rates would be required to precipitate the observed declines in pup production. Moreover, the small changes required would have a relatively modest effect on the age composition of females. Thus, I think its possible to make fairly reasonable inferences about the number, age-structure and biomass of the female northern fur seals.

Males are more problematic, and I consider the projections and estimates presented in this assessment to be more speculative. Due to the subadult male harvests, older males were under-represented in the population during the pelagic research program. In addition, little sampling was conducted at the more northerly latitudes where males tend to winter. As a result, insufficient numbers of male specimens were collected to estimate survival rates or fit growth curves. Some bulls were collected on land, but samples sizes were small, and potential sampling biases may have been large because social factors can play an important role in dictating which males occupy breeding territories. Moreover, the only yardstick for tracking the population dynamics of males are the counts of harem and idle territorial males, and this is fraught with problems. The territorial males represented only a small remnant (extremely small during harvests) of male cohorts recruited about a decade earlier. Moreover, its not known what proportion of older males are ashore, and the literature is somewhat ambiguous or vague on the subject[7]. Its clear the prevalence of males has increased since the harvests were terminated, but the magnitude of the increase could not be validated and warrants further investigation. The increased prevalence of older males could be important from an ecological perspective because, being considerably larger than females, they could potentially constitute a significant portion of the total population biomass (and hence prey consumption). Projection models suggest that males could now constitute about half the total biomass of fur seals, compared with about 20% at its lowest point during the intense male harvests in the 1970s. Inter-species comparisons with other fur seals, especially those never subject to male harvests, might be useful for delineating the normal range of sex ratios (Wickens and York 1997). Life tables for California and Steller sea lions – two other polygynous otariids - indicate that males, although numerically less abundant, comprise about 64% and 59% of the total biomass respectively owing to their larger body size (Olesiuk, unpublished data).

The underlying cause of the decline in pup production on the Pribilof Islands has not been identified. Direct human-induced mortality contributed to the declines in the 1960s, but has since played a negligible role. There continues to be a small subsistence take of subadult males, but at greatly reduced levels compared to the historic commercial harvests taken during while the herd flourished, and there is little evidence the male harvests adversely affected female reproductive rates (Gentry 1998). Entanglement could be a significant source of mortality, but its difficult to extrapolate mortality rates from entanglement rates, and entanglement appears to affect mainly males.

The lack of direct human-induced mortality that might explain the decline in pup production has shifted the focus to bottom-up or top-down ecological forcing mechanisms, such as nutritional stress resulting from reduced abundance or availability of prey, or increased predation levels or shift in the diet of killer whales. Obviously, the waters surrounding Pribilof Islands are critical to the species, as lactating females need to find adequate prey resources within commuting distance during a period of high energy requirements (Perez and Mooney 1986). However, the waters along the west coast of North America, including British Columbia, should also be regarded as important habitat. This is where the majority (74%) of reproductive females winter, and they spend about as much time in coastal winter feeding areas as they do on the Pribilof Islands. Moreover, pregnant females, like lactating females, have elevated energy requirements and appear to need to expend extra foraging effort during daylight hours to meet there needs (Perez 1996[8]). Females also exhibit a sharp increase in body mass during the latter part of the migration period (Trites and Bigg 1996), and these energy reserves may be important

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[7] In reference to the harem and idle bulls, Lander and Kajimura (1984), citing Chapman (1964), wrote that "*harem bulls of the Pribilofs spend about one quarter of their time at sea during the breeding season and idle bulls about half their time at sea and half on land*" whereas York (2005a) suggested it was "*tacitly assumed… that all males were present on land during the breeding season and that the count of males actually reflected their number, rather than an index of abundance*".

[8] Perez, M. A. 1996. Northern fur seal (*Callorhinus ursinus*) prey association and diel feeding behaviour determined from stomach contents. Unpublished Report. 70p.

for meeting lactation requirements. Thus, the abundance and availability of suitable prey in coastal wintering areas may be as important in sustaining fur seal population productivity as they are in the Bering Sea.

Northern fur seals are an opportunistic predator, and diets can change over time. The stomach samples used to asses diet were collected 30-50 years ago, and its possible diets have evolved since that time. While opportunistic, fur seals forage mainly on small schooling fishes (Perez and Bigg 1986), such as northern anchovy and herring. These prey stocks can change or cycle in abundance (Rodriguez-Sanchez et al. 2002), and there is evidence that sardines have been increasing in recent years, and have begun to appear in the diet of sea lions (Olesiuk, unpublished data). Northern fur seals may be consuming more sardines now compared with when the pelagic sampling occurred. Off Japan, for example, fur seal diets were also comprised mainly of small schooling fishes, including Japanese anchovy, during the pelagic collections, but shifted in the 1980s to Japanese sardines when those stocks recovered (Yoshida and Baba 1984). Thus, the diet information should be interpreted in general terms (small schooling fishes) rather than specific prey species.

The prey resources utilized by fur seals are similar to those utilized by other pinnipeds, which also target small schooling fishes. Although fur seals and sea lions may not directly compete, they often are dependent on the same prey stocks. The only unique feature of fur seal diets is the greater prevalence of gonatid/onychotuethid squid, which are taken mainly in offshore areas. Small schooling forage fish are also important in the diets of sea lions, but they tend to have a more diverse diet (Gentry 1998), and diversity may be directly correlated with population resilience (Merrick et al. 1997). In any event, pinniped populations along the west coast of North America have certainly not declined like the concurrent declines that occurred in the Gulf of Alaska and Bering Sea (Trites et al. 2007).

Female northern fur seals in the northeastern Pacific Ocean may be facing increasing competition for prey resources. In the 1960s and 70s, few males survived to adulthood, and the Pribilof Island stock was dominated by females, which constituted about 80% of the total population biomass. Moreover, about half the male biomass was comprised of juveniles that were too young animals to migrate back to the Pribilof Islands. With the cessation of commercial harvests, the prevalence of males has increased and they may now constitute nearly half the total population biomass. The increase is largely due to the increase in number of adult males, many or most of which do return to the Pribilof Islands during the breeding season. The early Russian sealers seemed to have figured out – apparently without input from scientists or managers – that productive fur seal herds could be maintained by removing males, leaving prey resources for females. There is a large body of scientific evidence indicating that the removal of most males had little if any effect on female reproductive rates (Gentry 1998). However, it is less clear whether the recent increase in prevalence of surplus males may be adversely affecting the reproductive performance of females.

Female northern fur seals in the northeastern Pacific Ocean may also be facing increasing competition for prey resources on their winter feeding areas. In the 1960s and 1970s, fur seals were the dominant predator along the west coast, both in terms of numbers and biomass. However, with the recovery of sea lion populations, which had been depleted by over-hunting and predator control programs, this has changed dramatically. The biomass of fur seals has dropped from about 3-times the combined biomass of the two species of sea lions, to about one-third the biomass of sea lions. Interestingly, sea lion populations in the northwestern Pacific

Ocean have not exhibited such increases, which might help explain why western stocks of fur seals have not declined.

While this report suggests that intra- and inter-specific competition for prey resources could potentially affect the status of northern fur seals, a thorough assessment was beyond the scope of this study, and the subject warrants further investigation. An important element that, unfortunately, was ignored due to time constraints, was the competition for prey resources with commercial fisheries. Future studies need to consider the size, productivity and distribution of major prey stocks, such as anchovy and herring, to assess their ability to support apex predators, including humans. This could have important implications for the recovery potential of northern furs seals, and such assessments should be included as part of northern fur seal conservation or management plans.

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TABLES

Table 1. Estimated changes in northern fur seal pup production over the last 30 decades (3 generations) from 1972-1976 to 2002-2006. See text for details and data sources.

Rookery	**1972-1976**	**2002-2006**	**Population Trend**
Pribilof Islands[9]	346,900	150,700	2.7% decline per year
Commander Islands	62,800	59,800	Little net change
Kuril Islands	10,500	28,600	3.0% increase per year
Robben Island	33,500	28,200	No net change (fluctuated)
Bogoslof Island	-	12,600	Rapid growth since 1980
San Miguel Island	580	2,150	Increases interrupted by *El Nino's*
Total	**454,280**	**282,050**	**~38% Decline**

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[9] Sea Lion Rocks off St. Paul Island was not routinely surveyed, so I assumed it accounted for 4.9% of total pup production on the Pribilof Islands based on its average contribution in years it had been surveyed during 1966-2000 (range 4.3% - 5.7%).

Table 2. Multipliers for estimating total stock size (and components of the stock) during subadult male harvests (Kenyon *et al.* 1954; Lander 1981) and adjusted for unexploited populations (Loughlin *et al.* 1994) (see York 2005a for computation methods). The range of multipliers is also given for St. Paul Island during 1972-1976 and 2002-2006 based on model projections (Section 2.2). Mature individuals represent the number of females aged 4+ years and males aged 6+ years in the population. Mean body mass was calculated from sex- and age-structure as per Equation 3 (see text).

Population Component	**Harvested (Kenyon *et al.* 1954)**	**Havested (Lander 1980)**	**Unexploited (Loughlin *et al.* 1994)**	**St. Paul Island (1972-76) (Section 2.2)**	**St Paul Island (2002-2006) (Section 2.2)**
Pups (both sexes)	100.00	100.0	100.00	100.0	100.0
Yearlings (both sexes)	40.00	48.90	50.00	43.74	48.38
Age 2 year (both sexes)	32.00	38.10	40.00	35.96	37.36
Females age 3 yrs	166.67	16.80	17.20	17.87	18.10
Females aged 4+ yrs		145.59	166.67	150.20	151.69
Males age 3-5 yrs	8.29	24.25	43.20	12.67	36.55
Males aged 6+ yrs	3.34	6.6	30.40	2.92	33.20
Total animals	334.29	380.24	447.47	363.36	422.33
Mature individuals	~153.21	152.19	197.07	153.12	184.88
Mean body mass (kg)	-	23.3	28.7	21.0	28.9

Table 3. Estimated changes in total abundance of northern fur seal stocks and number of mature individuals in the population over the last 30 decades (3 generations) from 1972-1976 to 2002-2006.

Rookery	1972-1976			2002-2006		
	Pup Count	**Multiplier**	**Stock Size**	**Pup Count**	**Multiplier**	**Stock Size**
Pribilof Islands	346,900	3.61	1,250,000	150,700	4.22	636,000
Commander Islands	62,800	3.80	239,000	59,800	4.47	268,000
Kuril Islands	10,500	4.47	47,000	28,600	4.47	128,000
Robben Island	33,500	3.80	127,000	28,200	4.47	126,000
Bogoslof Island	-	-	0	12,600	4.47	56,000
San Miguel Island	580	4.00	2,300	2,150	4.00	8,600
Total Abundance			**1.67 million**			**1.22 million**
Mature Individuals			**699,000**			**537,000**

Table 4. Estimated abundance of northern fur seals and other pinnipeds in the North Pacific Ocean, and in coastal waters off British Columbia. Northern fur seal estimates were obtained from Table 3 and Section 3.4; harbour seals estimates were obtained from Burns (2002), Brown (1997), Jeffries *et al.* (2003), Carretta *et al.* (2007), Angliss and Outlaw (2007), and Olesiuk (2007); California sea lion estimates were obtained from Lowry and Maravilla-Chavez (2003) and Olesiuk (2003); Steller sea lion estimates were obtained from Angliss and Outlaw (2007), Burkanov and Loughlin (2007), and Pitcher *et al.* (2007); northern elephant seal estimates were obtained from Carretta *et al.* (2007), with the numbers occurring in BC waters unknown. The table does not include the ice seals (spotted seals, ribbon seals, ringed seals, and bearded seals) that generally occur in the Bering Sea and Sea of Okhotsk, although distributions may extend into the North Pacific Ocean.

Species	**North Pacific**	**British Columbia**
Northern fur seals	1.22 million	123,000
Harbour seals	367,000	99,400
California sea lions	240,000	2,000-3,000
Steller sea lions	113,000	18,400 -19,700
Northern Elephant seals	101,000	100’s ??

Table 5. Magnitude of changes in key vital rates required to cause a 2% decline in pup production, and the effect of the change in each vital rate on the pup multiplier (both sexes combined) for estimating total abundance and on mean body mass.

Parameter	**Δ%**	**Multiplier**	**Mean Body Mass (kg)**
Juvenile survival	82%	4.07	28.8
Adult survival	92%	4.21	29.5
Pregnancy Rate	88%	4.39	27.7

FIGURES

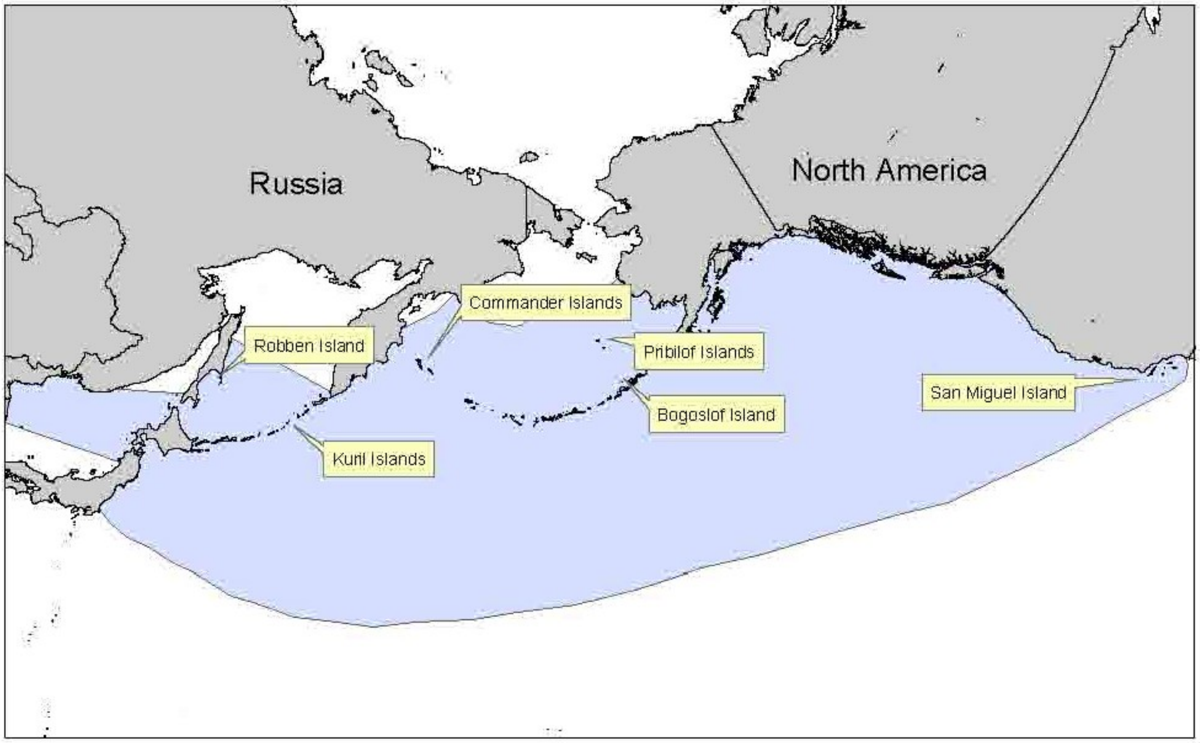


Figure 1. Range of northern fur seals showing location of breeding rookeries and pelagic distribution during migrations (from NMFS 2006).

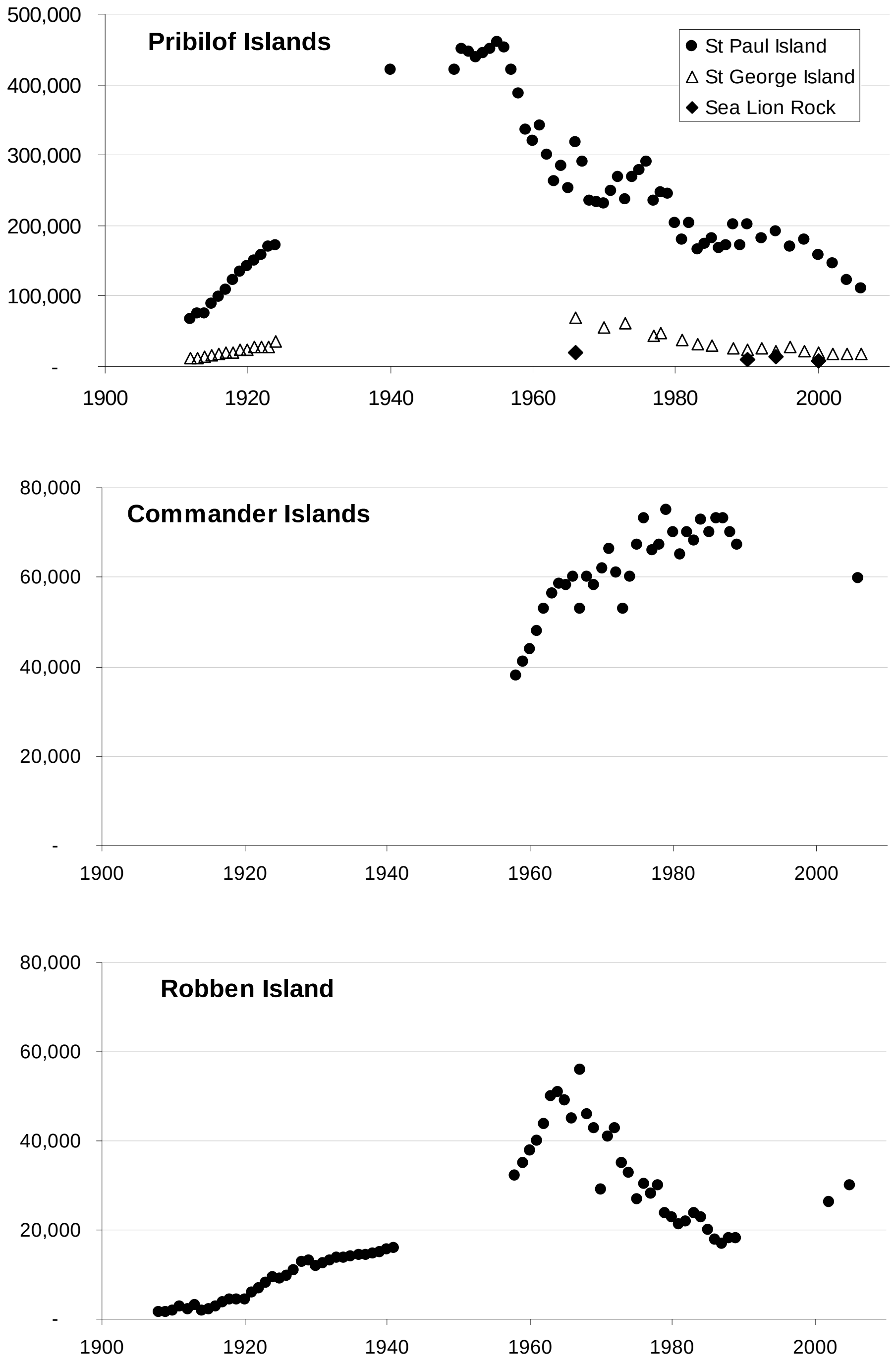


Figure 2 (continued on next page). Northern fur seal pup counts on rookeries at: a) Pribilof Islands; b) Commander Islands; c) Robben Island; d) Kuril Islands; e) Bogoslof Island; and f) San Miguel Island. Note that counts are plotted on varying scales for each rookery depending on its size.

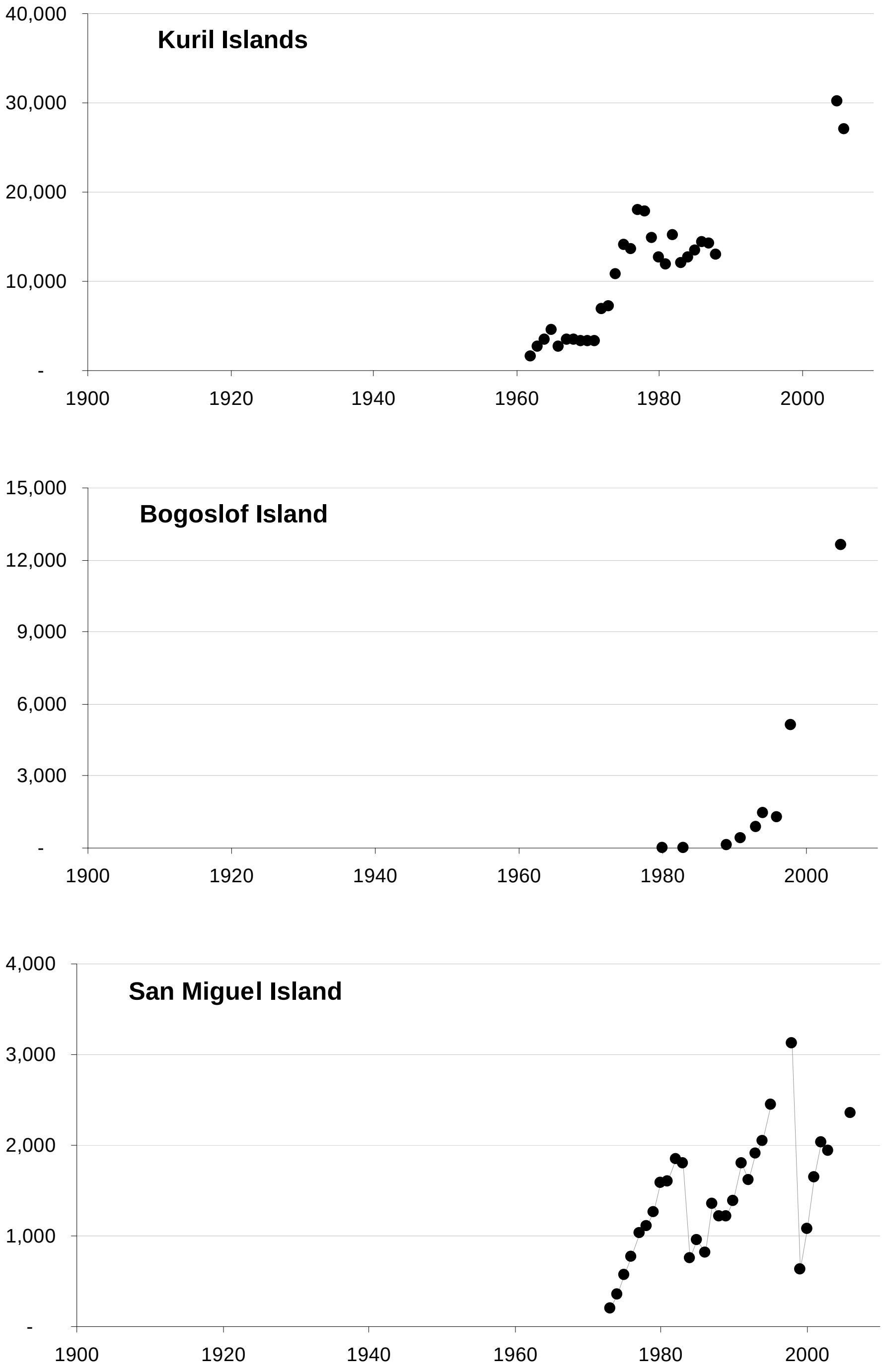


Figure 2 (continued from previous page). Northern fur seal pup counts on rookeries at: a) Pribilof Islands; b) Commander Islands; c) Robben Island; d) Kuril Islands; e) Bogoslof Island; and f) San Miguel Island. Note that counts are plotted on varying scales for each rookery depending on its size.

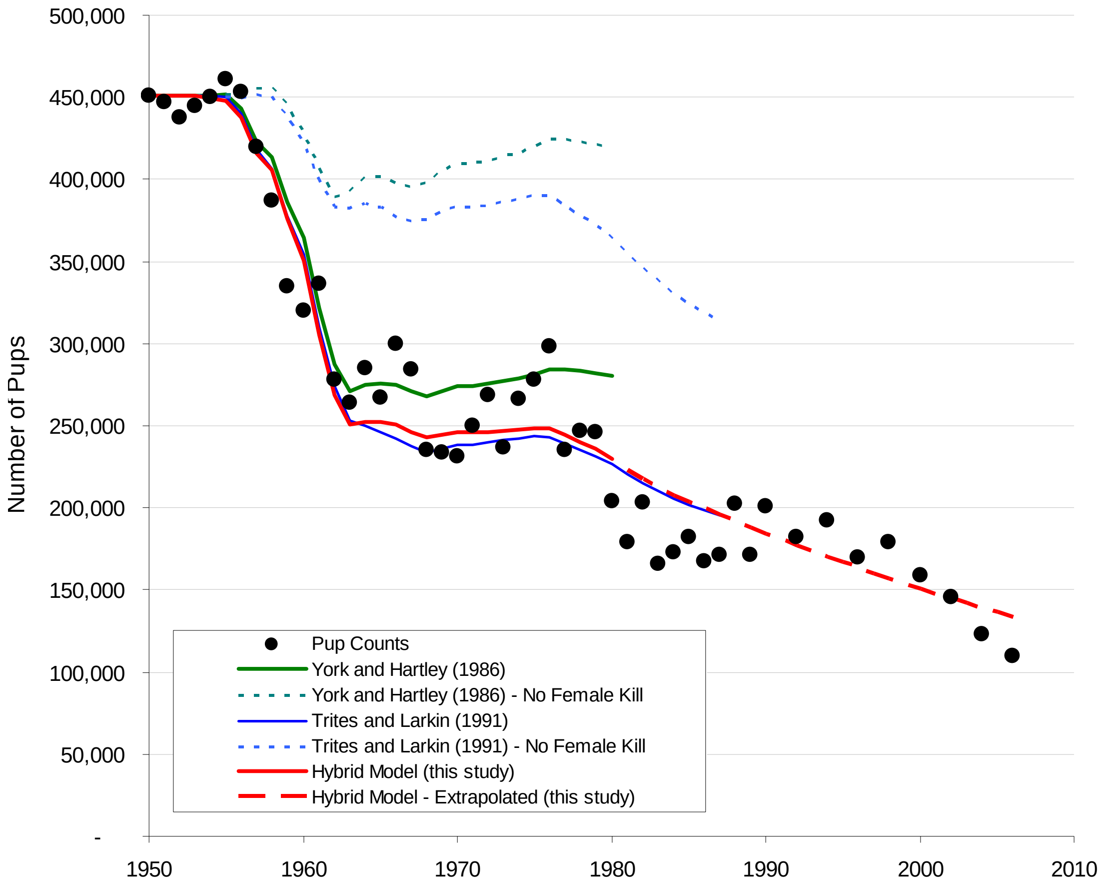


Figure 3. Pup counts and predicted pup production on St. Paul Island based on projection models. The green line shows predicted pup counts based on the York and Hartley (1981) model with (solid line) and without (dashed line) the females removals in the herd reduction program during 1956-68 and pelagic research collections during 1958-74. The blue lines show the same projections for the Trites (1984) and Trites and Larkin (1989) model. The primary difference between the two models is that York and Hartley (1981) assumed juvenile survival was higher for females than males, whereas Trites and Larkin (1991) assumed survival of females was equal to males. The red line shows projections for the hybrid model used in this study that incorporated York and Hartley's (1981) pregnancy and adult (age 2+) survival schedules and Trites (1984) annual juvenile survival rates. The dashed reds line shows extrapolated values assuming that juvenile survival remained at the average levels observed during the last decade data were available. See text for details.

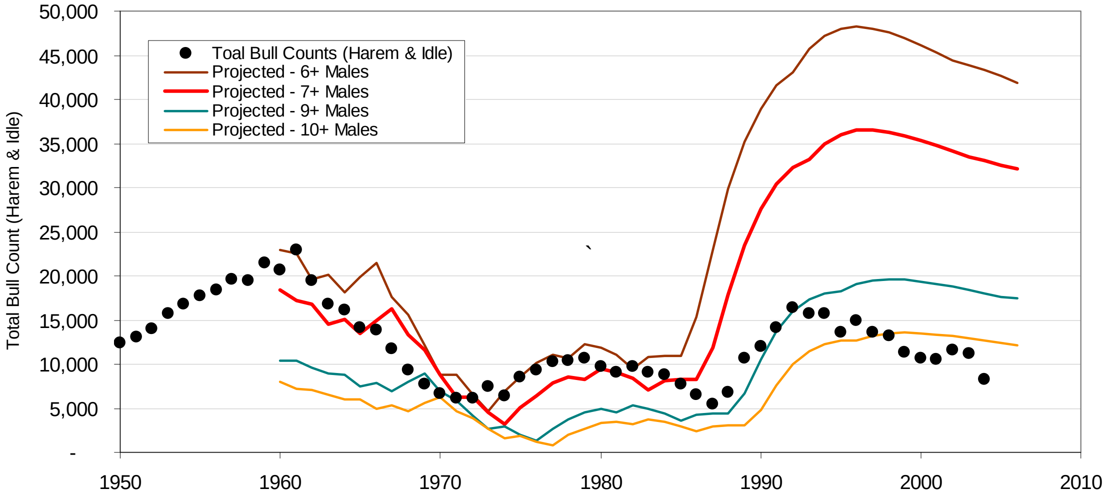


Figure 4. Total bull counts (harem and idle) for St. Paul Island compared to projected changes in the prevalence of males aged 6+ years, 7+ years, 9+ years, and 10+ years. The projections suggest that prior to the termination of male harvests in 1984, most of the males aged 6-7 years were occupying territories. More recent projections suggest a smaller proportion of males are holding territories, or that the age of territorial males has increased, or that mortality or dispersal rates have increased.

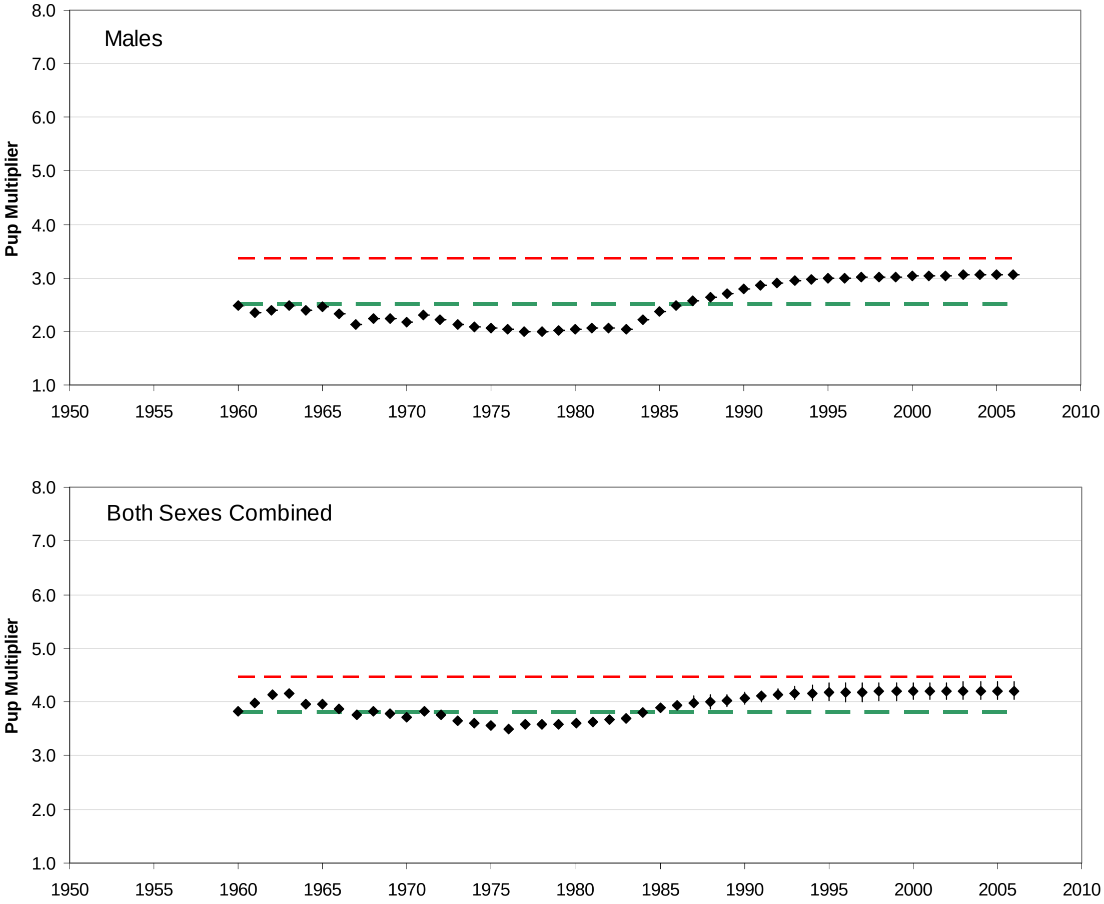


Figure 5. Projected changes in the pup multiplier (i.e. ratio of total number of animals to pups) for: a) females; b) males; and c) both sexes combined. The vertical bars represent the uncertainty for females depending of what vital rates were varied to emulate a 2% rate of decline in pup production. Dashed horizontal lines represent the values predicted by life tables for an unexploited population (red lines; Loughlin *et al.* 1994) and harvested population (green lines; Lander 1981).

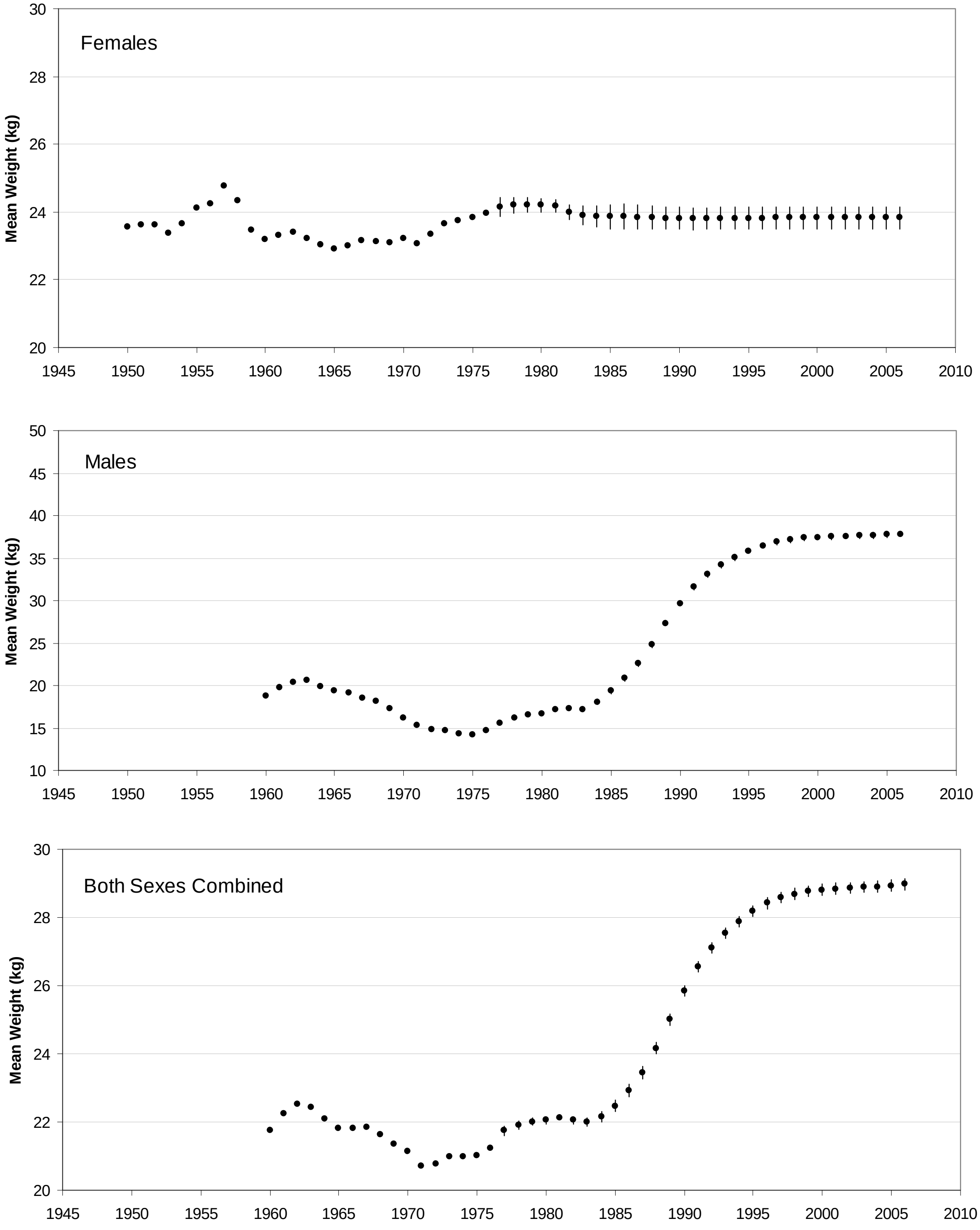
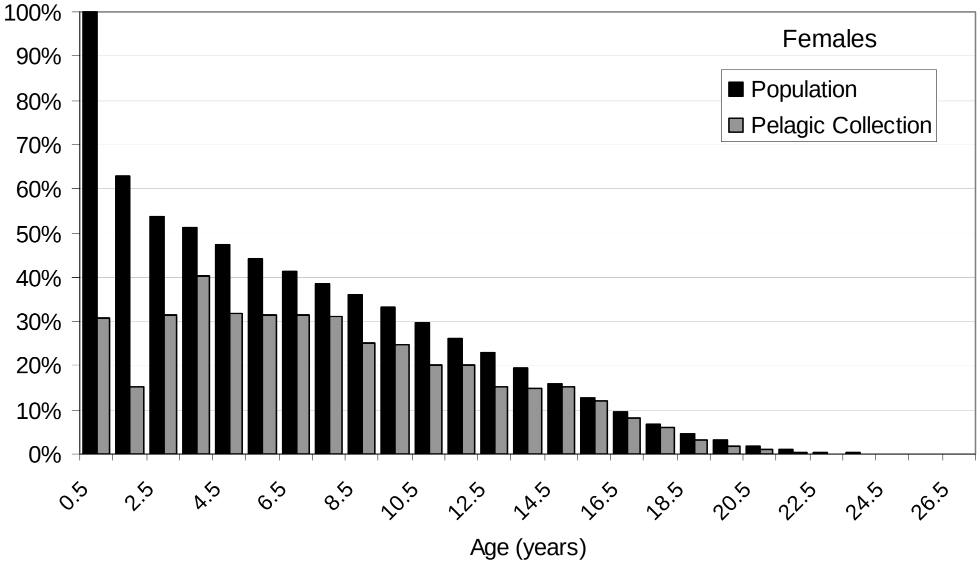


Figure 6. Projected changes in mean biomass of: a) females; b) males; and c) both sexes combined. The vertical bars represent uncertainty for females depending of which vital rate was varied to emulate a 2% rate of decline in pup produciton.



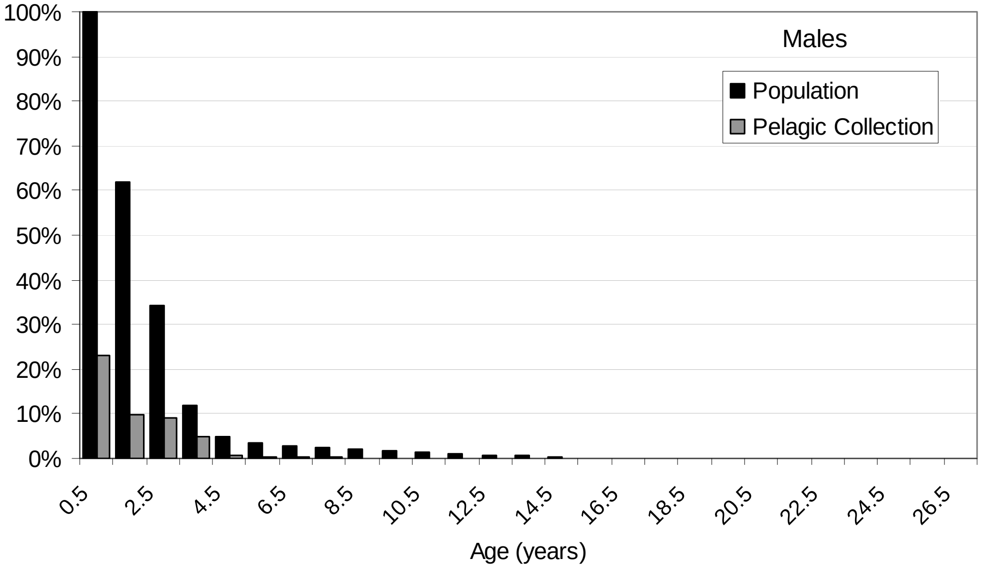


Figure 7. Predicted age-composition for females (top) and males (bottom) in the population during 1958-74 based on the St. Paul Island projections (black bars). The grey bars show the relative frequency distribution of the 18,449 specimens collected off the west coast of North America during the pelagic research program during 1958-74. Based on satellite tracks (Ream *et al.* 2005; R. Ream, NMML, Seattle, pers. comm.), it was assumed that 75% of females aged 8+ wintered in coastal areas (see Section 4.3).

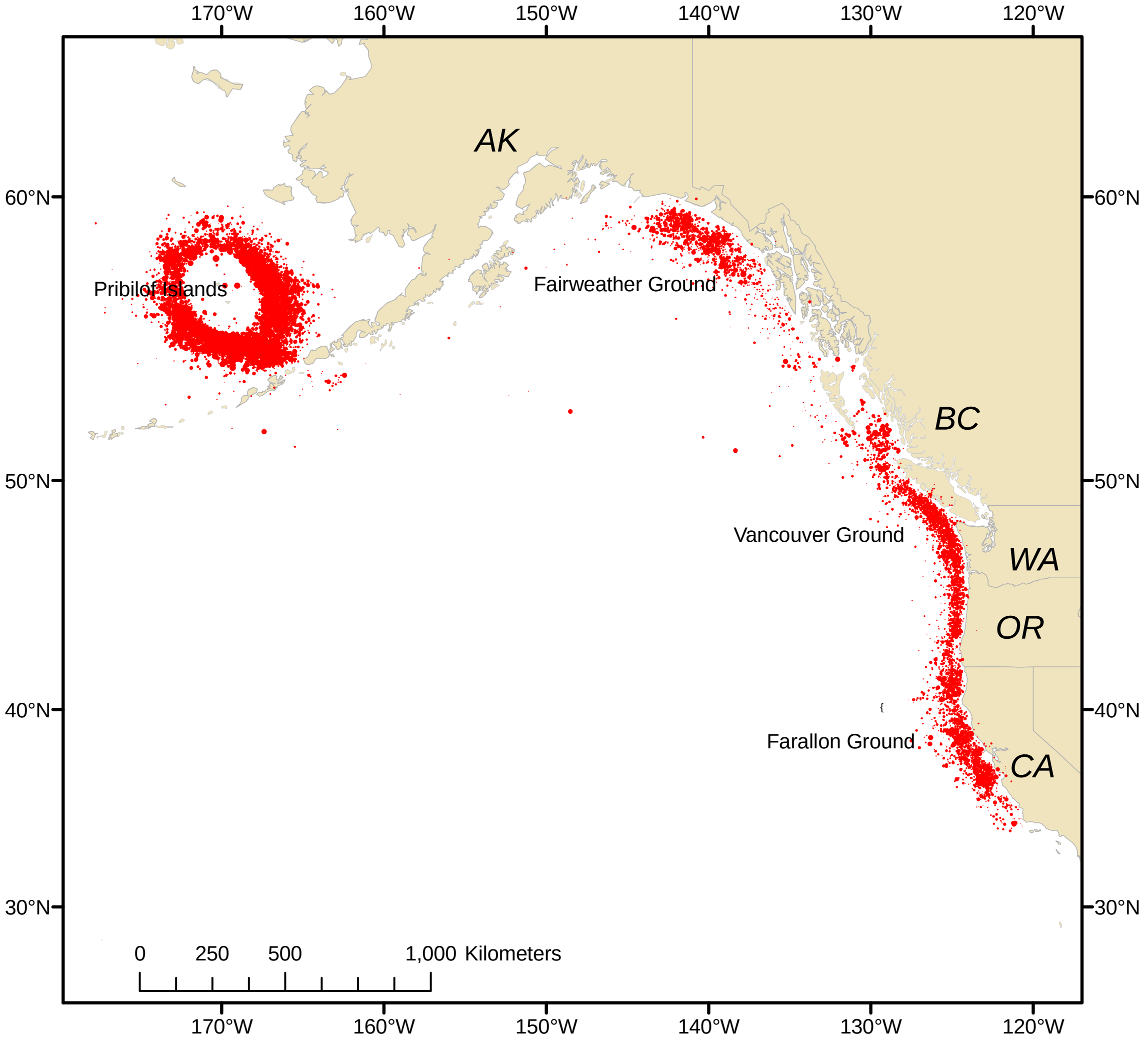


Figure 8. Overview map showing the distribution of fur seals harvests (*n*=258,120 seals) during pelagic sealing from 1891-1911, with the main hunting areas also noted (data from Murie 1981).

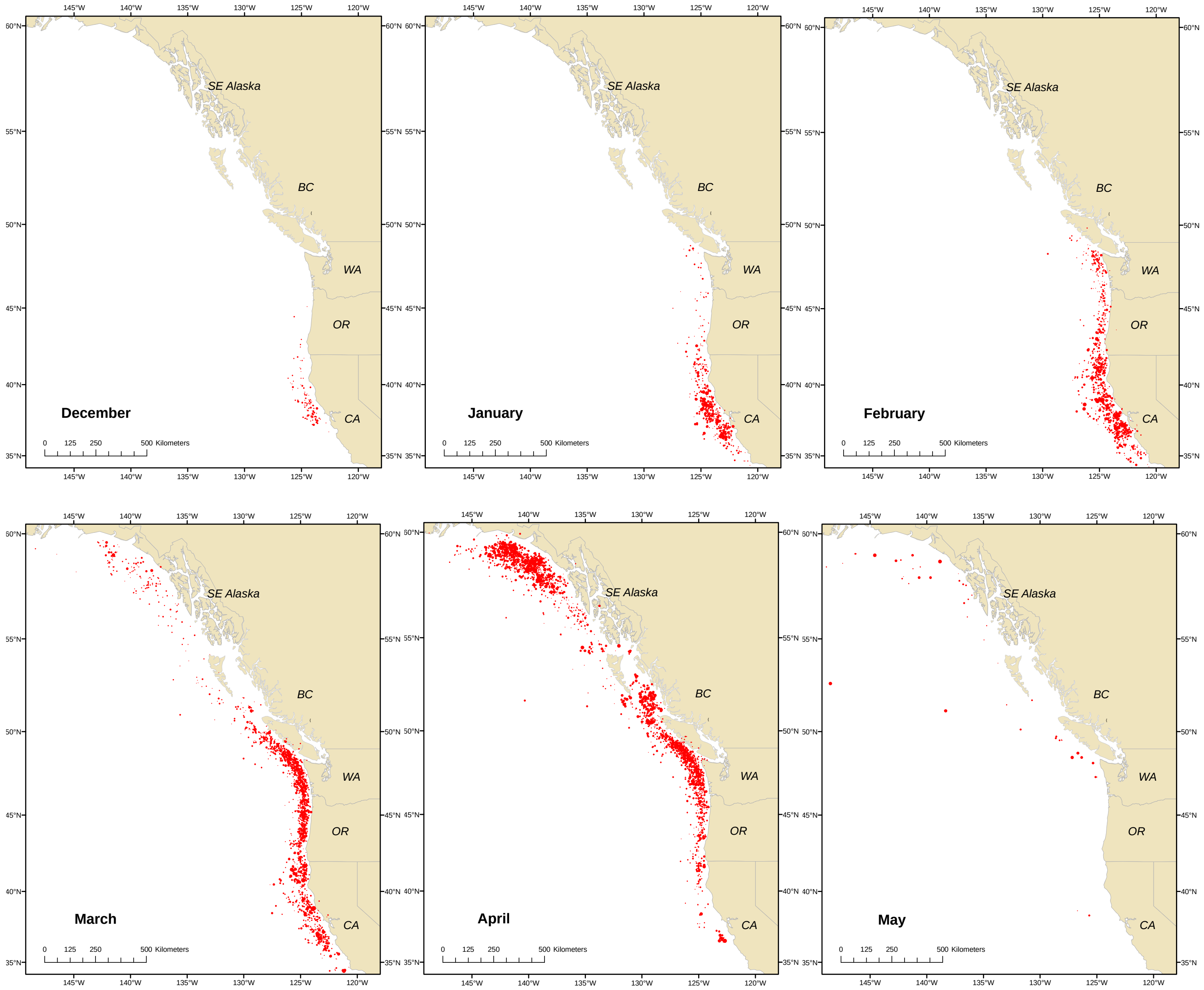


Figure 9. Seasonal shift in distribution of pelagic sealing kills during 1891-1911 (data from Murie 1981).

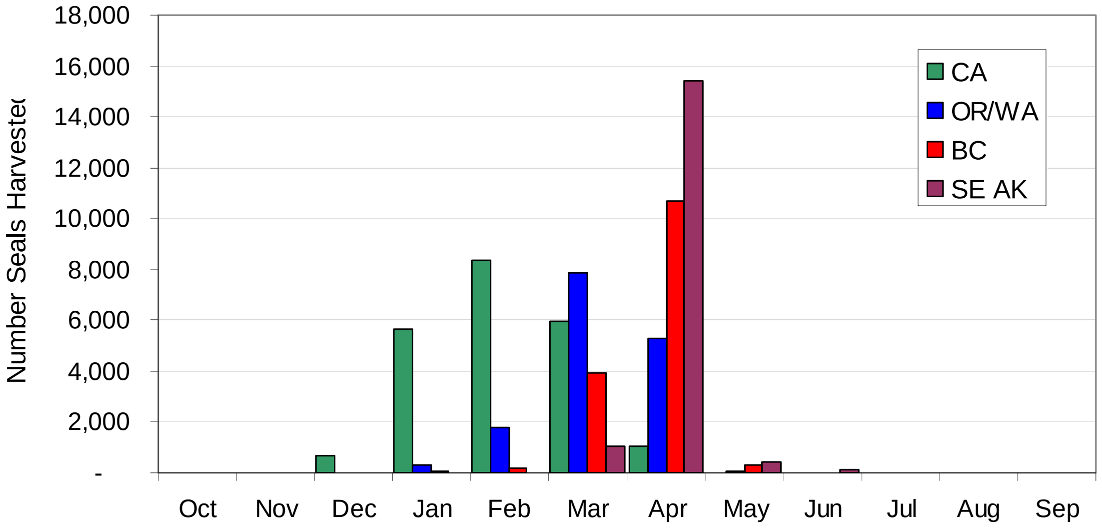


Figure 10. Seasonal distribution of fur seal harvests by region along the west coast of North America during 1882-1911 (based on data in Murie 1981).

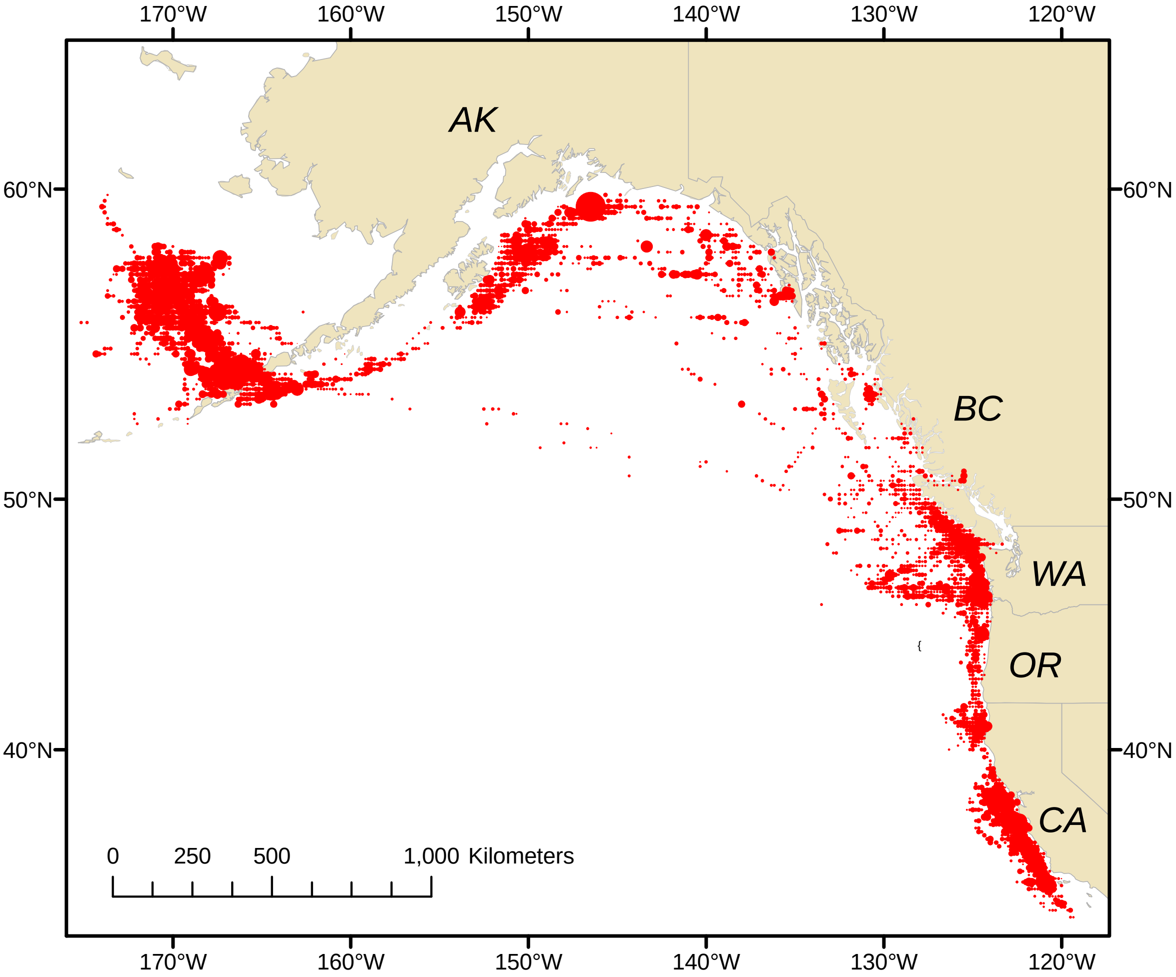


Figure 11. Overview map showing relative distribution of fur seal sightings (number of seals seen per hour) during pelagic research trips from 1958-1974. Data represent 37,221 sightings during 14,600 hours of observations.

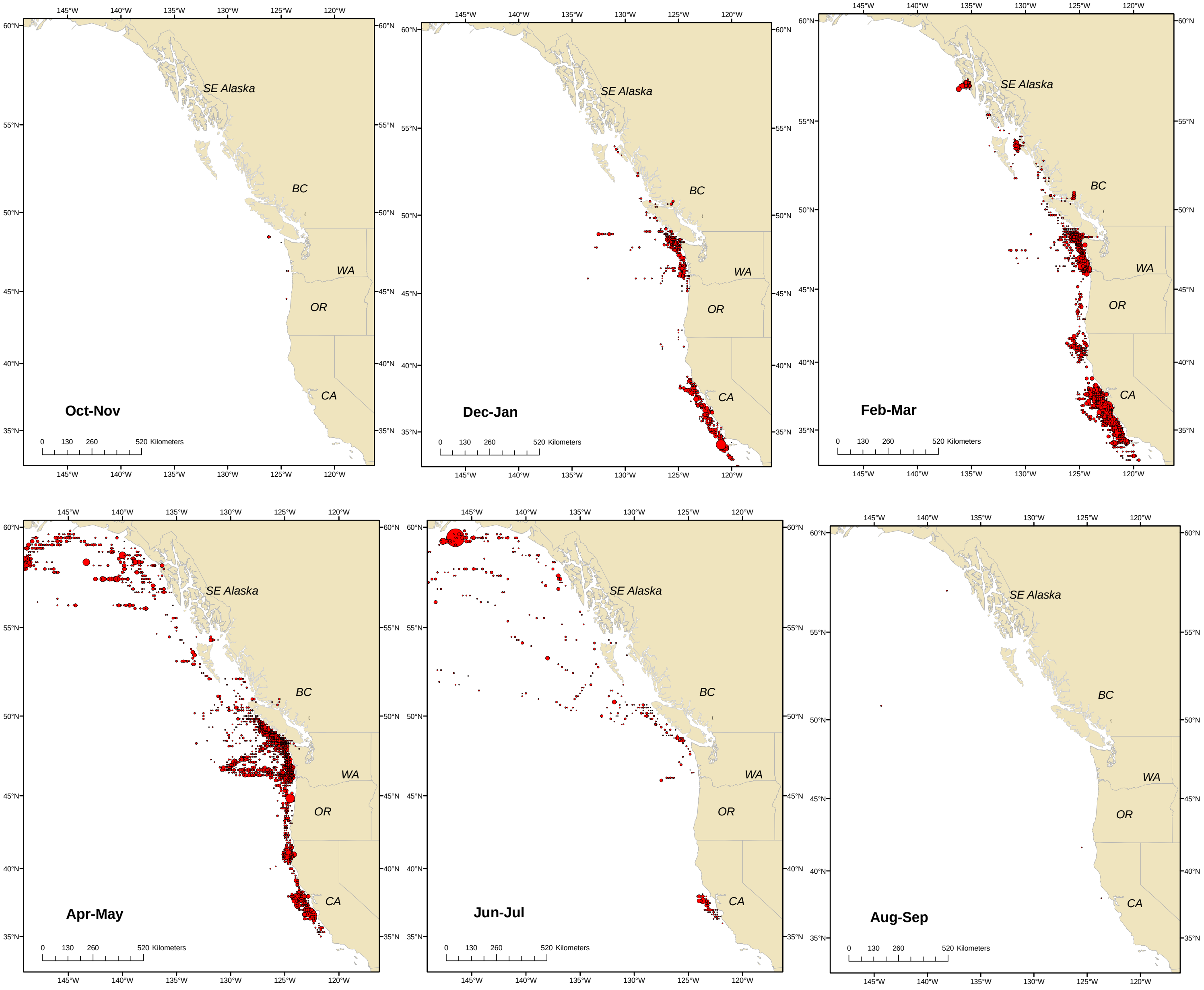


Figure 12. Maps showing seasonal shift in relative distribution of fur seal sightings during pelagic research trips from 1958-1974.

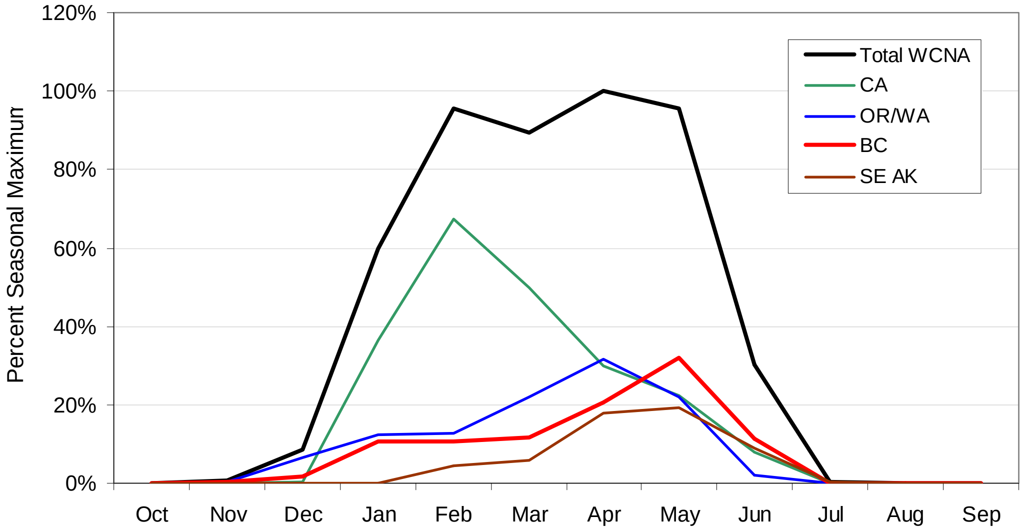


Figure 13. Relative distribution of northern fur seals by region along the west coast of North America. Relative abundance was calculated for each region based on the average number of seals sighted per hour for all years combined multiplied by the size of each region (see Antonelis and Perez 1984 for details). Relative numbers of animals present is expressed as a proportion of the seasonal peak in April.

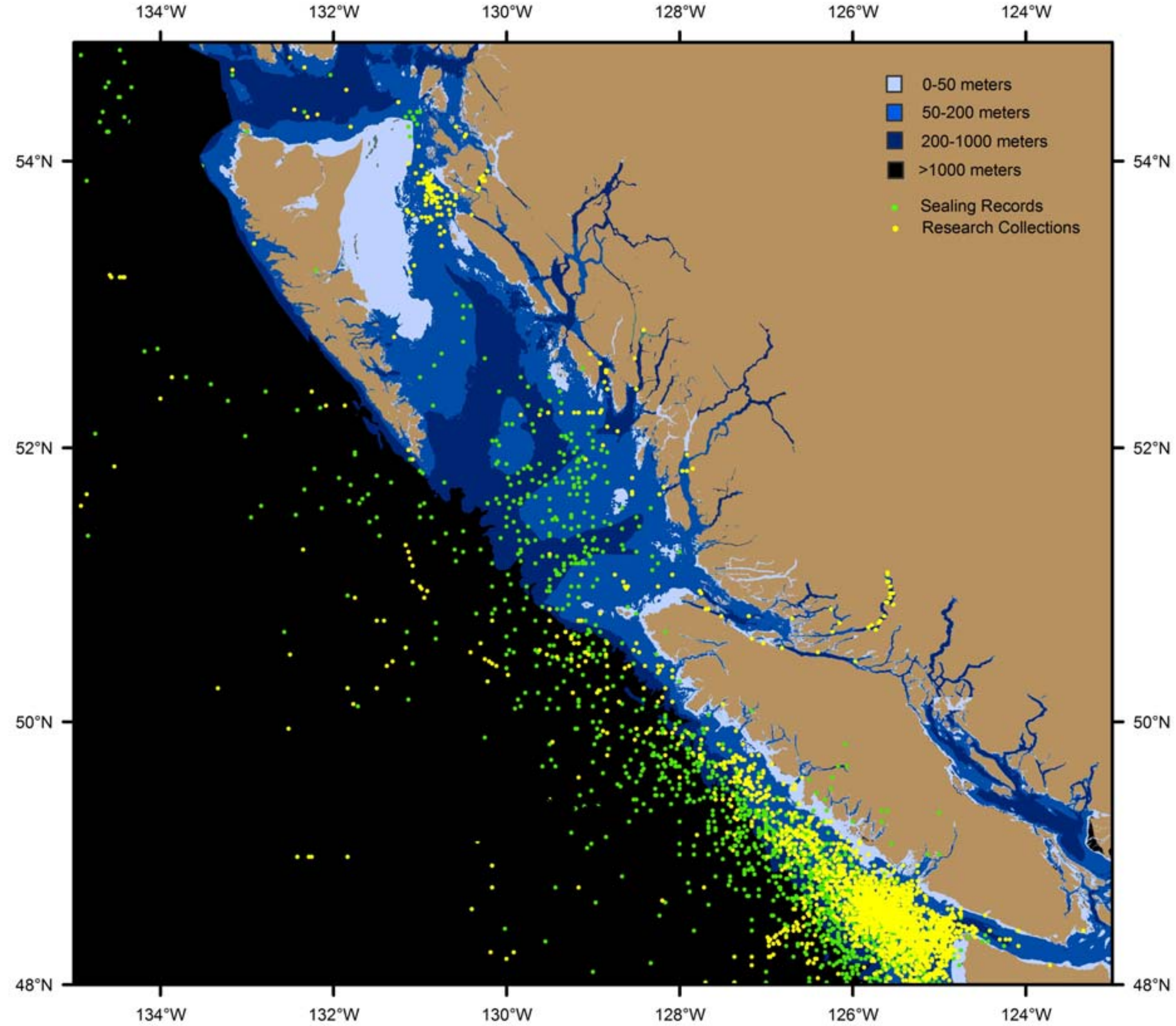


Figure 14a. Main wintering distribution of northern fur seals in Canadian waters based on sealing records from 1891-1911 and pelagic research collections during 1958-74.

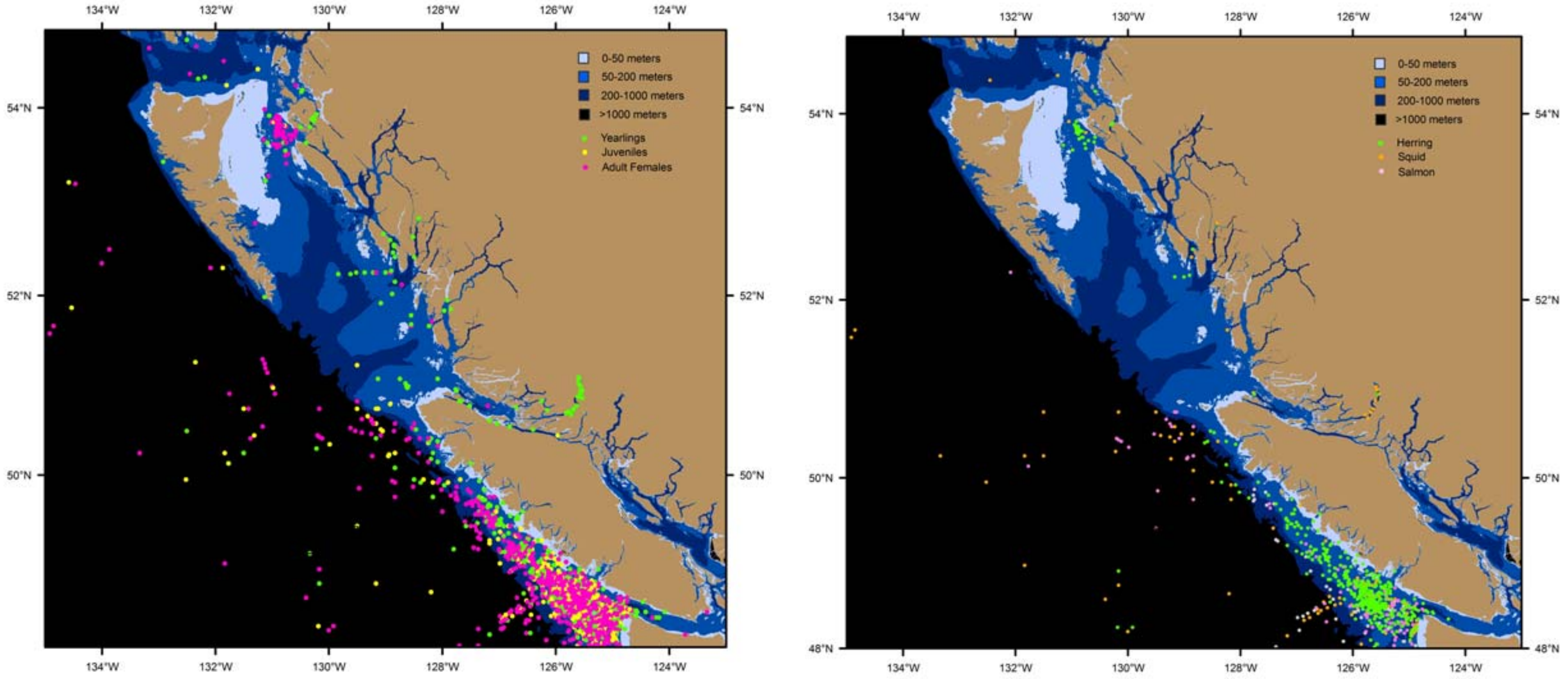


Figure 14b. Fur seal utilization of wintering habitat in Canadian waters based on distribution of pelagic research collections during 1958-74. The left panel shows distribution by sex and age category, and the right panel shows the distribution of key prey species for seals with non-trace prey in stomachs.

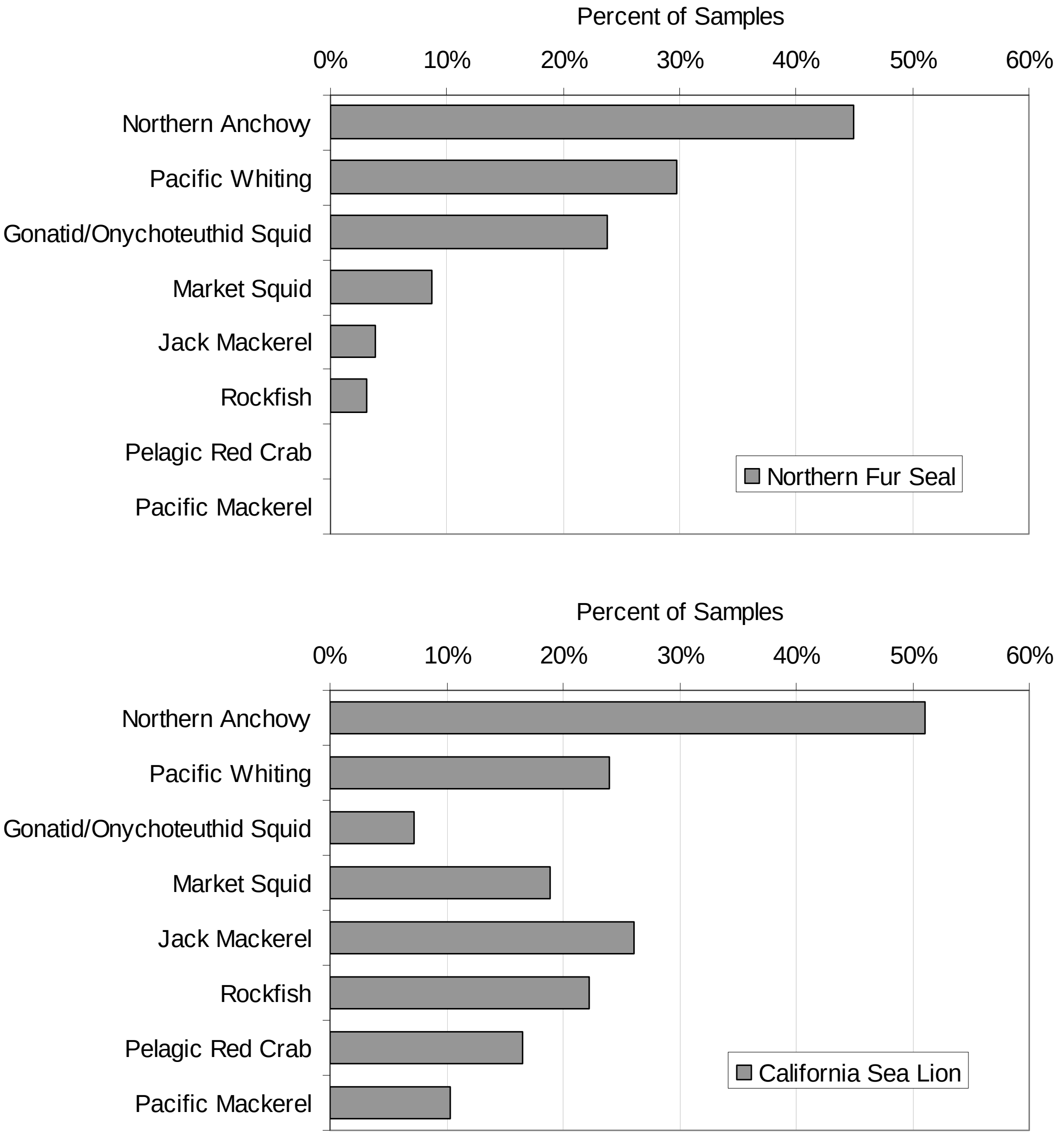


Figure 15a. Comparison of key prey species for northern fur seals wintering off California (top; *n*=1,757 stomach samples with non-trace prey) and California sea lions on the Channel Islands throughout the year (bottom; *n*=2,394 scat samples with identifiable prey, from Lowry *et al.* 1990, 1991). Key prey were defined as those that occurred in at least 10% of samples of either predator.

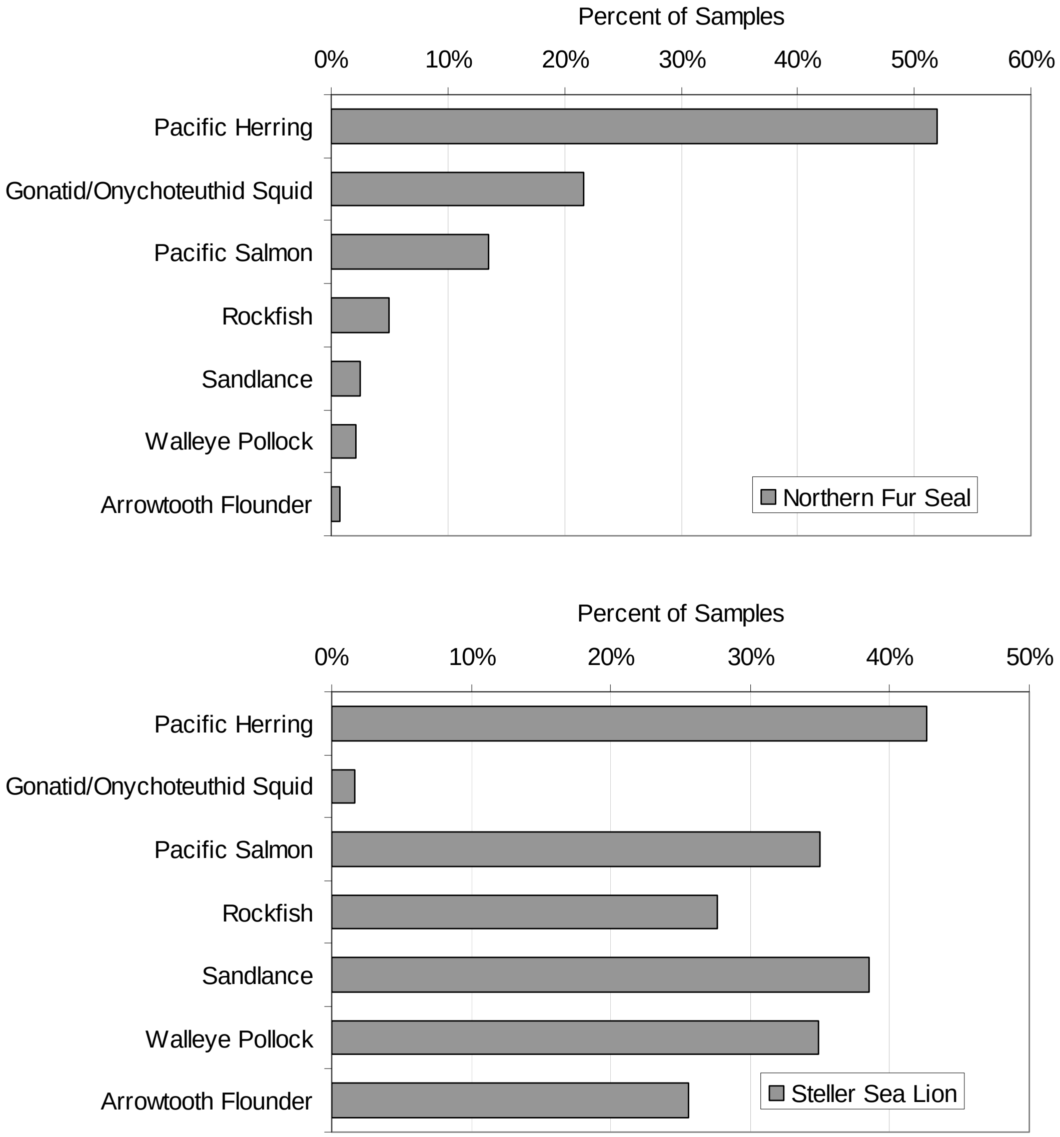


Figure 15b. Comparison of key prey species for northern fur seals wintering off British Columbia and SE Alaska (top; *n*=1,355 stomach samples with non-trace prey) and Steller sea lions in British Columbia and Forrester Island, mainly during the summer breeding season (bottom; *n*=2,481 scat samples with identifiable prey, Trites and Olesiuk, unpublished data). Key prey were defined as those that occurred in at least 10% of samples of either predator.

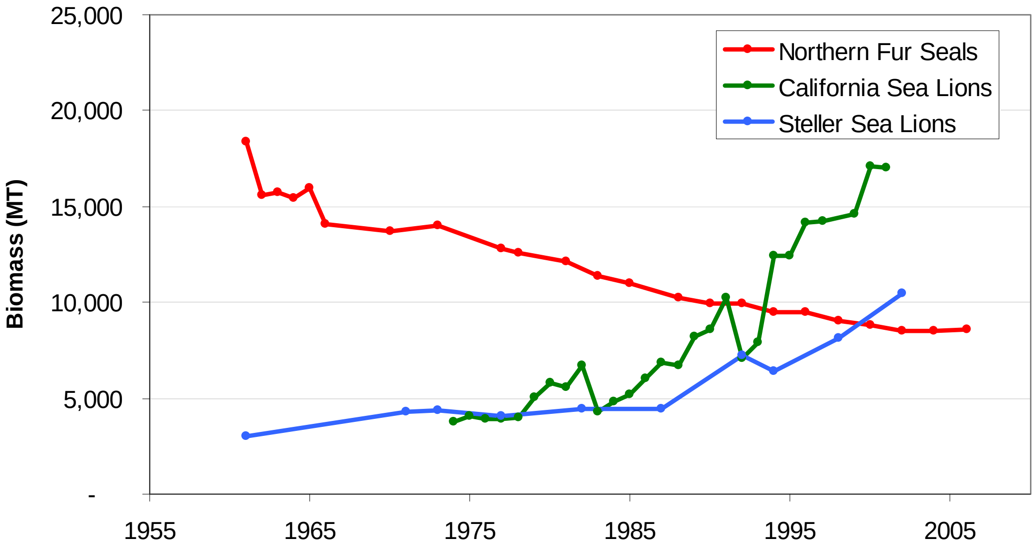


Figure 16. Recent changes in the biomass of northern fur seals and sea lions off the west coast of North America. Abundance of each species was estimated by applying appropriate multipliers to pup counts at breeding sites. California sea lion trends are from Lowry and Maravilla-Chavez (2005) and Steller sea lion trends are from Pitcher *et al.* (2007). Depressed California sea lion pup counts during the severe *El Nino* event in 1998 was excluded. Biomass was calculated from life tables and growth curves as described in the text (Olesiuk, unpublished data).

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ERRATUM

Olesiuk, P.F. 2008. Preliminary Assessment of the Recovery Potential of Northern Fur Seals (*Callorhinus ursinus*) in British Columbia. DFO Can. Sci. Advis. Sec. 2007/076.

The two paragraphs below have been removed from page 25 because the assessment of COSEWIC status falls outside the scope of a Recovery Potential Assessment. The online version has been updated accordingly.	Les deux paragraphes ci-dessous ont été supprimés de la page 25 du fait que l'évaluation de la situation faite par le COSEPAC ne cadrait pas avec la portée d'une évaluation du potentiel de rétablissement. La version en ligne a été mise à jour en conséquence.
Paper copies of this Research Document were distributed on December 8, 2008. Please replace the cover page to page 40 with the attached, and keep the original tables and figures.	Des exemplaires sur papier de ce document de recherche ont été distribués le 8 décembre 2008. Veuillez remplacer de la page couverture jusqu'à la page 40 par le document ci-joint et conserver les tableaux et les figures d'origine.
We apologize for any inconvenience this may cause.	Nous nous excusons des inconvénients pouvant découler de cette situation.

Based on the estimated change in total abundance of northern fur seals, and change in number of mature individuals in the population derived in this assessment, the species does not appear to meet any of the COSEWIC criteria for listing as *threatened* or *endangered*. Fur seals are abundant and widely distributed – more so than any other pinniped in the North Pacific Ocean. The recent declines have been localized to one stock, and the overall decline in total abundance and number of mature individuals does not meet the threshold of "*an observed, estimated, inferred or suspected population size reduction of* $\geq$*30% over the last 10 years or three generations, whichever is the longer, where the reduction or its causes may not have ceased OR may not be understood OR may not be reversible*".

While northern fur seals may not meet COSEWIC thresholds for listing, the ongoing declines on the Pribilof Islands represents a serious conservation concern. The Pribilof Islands support the largest breeding stock, origin of many of the animals emigrating to new rookeries, and source of most animals wintering in Canadian waters. The declines seem to be a chronic problem extending back at least 50 years. The first symptom of reduced productivity was the slowing of the recovery of the population in the 1940s. Population growth fell below expectations, even though numbers were still depleted relative to pristine abundance levels. This led to the ill-fated removal of females during the herd reduction program, which certainly attenuated the declines in the 1960s, but it appears juvenile survival was below equilibrium levels and some decline would have occurred even in the absence of these kills. Surprisingly, the Pribilof herd has exhibited no signs of recovery following the herd reduction, and pup production has continued to decline up to the most recent pup count in 2006.