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# Population Viability Analysis for Northern Fur Seals (*Callorhinus ursinus*) in Canada

# Analyse de la viabilité de la population d'otaries à fourrure du Nord (*Callorhinus ursinus*) au Canada

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## ABSTRACT

A population viability analysis (PVA) was conducted for northern fur seals to assess risk of extirpation in Canada. The PVA is based on the diffusion model developed by Dennis et al. (1991) that projects populations along a trajectory based on recent trends with drift due to natural variability. The North Pacific fur seal population was considered a meta-population, with each breeding site representing a subpopulation (the smallest breeding site at San Miguel Island was excluded from the analysis). Recent trends for each subpopulation were estimated from pup counts using density independent or dependent models, and unexplained variation was assumed to represent natural variability (demographic stochasticity or environmental variability) after adjusting for measurement error. Models were fitted to the most recent 10-year, 30-year and 50-year time-series of pup counts. Monte Carlo techniques were used to project each subpopulation 200 years into the future, and risk of quasi-extinction estimated for the first 100 years. The threshold for quasi-extinction was set to an effective population size of 1,000 animals required to sustain genetic diversity, which for a polygamous species like the northern fur seal represents a total subpopulation size of 8,000 seals. I adopted a precautionary approach, and considered subpopulations to be endangered if there was a 1% chance of falling to quasi-extinction levels within the next 100 years, and threatened if there was a 20% chance of becoming endangered within the next 20 years. Tagging data were analyzed to determine the contribution of each subpopulation to abundance in Canada based on the propensity of animals from each breeding site to migrate along the west coast of North America. The threshold for quasi-extinction of the population and segment migrating through Canadian waters was set to the minimum viable population (MVP) size, which was 7,000 adults or 10,000 seals. The PVA indicated that all subpopulations are presently secure with little risk (0.00%-0.42%) of extirpation within the next century. The Pribilof Island subpopulation, the largest breeding site and source of the majority of animals migrating through Canadian waters, has been declining for the past 50 years. However, due to its large size, it is not at risk of extirpation within the next 100 years, but the probability of quasi-extinction will escalate if the declines persist beyond the next century. As the Pribilof Island subpopulation declines, animals from other breeding sites that are have been stable or increasing will play an increasingly important role in maintaining a MVP in Canada, and there appears to be no discernible risk of extirpation from Canadian waters. Currently, it is estimated that 75% of seals migrating through Canadian waters originate from the Pribilof Islands, compared with 97% when the pelagic research collections made in 1958-74. An estimated 15% of seals in Canada originate from the rapidly growing breeding site established on Bogoslof Island in 1980, and 8% from the Commander Islands where numbers have increased over the last 50 years but are now stable, and less than 1% from the growing but distant breeding sites in the Kuril Islands and Tuleny (Tyuleniy) Island. The assessment indicates that risk of extinction is a function of population size, trend and degree of natural variability, and that PVA provides a means of integrating such information. Population trend in itself is not a meaningful criterion for assessing risk, particularly for very large populations like the northern fur seal. Indeed, the northern fur is expected to continue to be the most abundant and widely distributed pinniped in the North Pacific.

# RÉSUMÉ

Une analyse de la viabilité de la population d'otaries à fourrure du Nord a été effectuée afin d'évaluer le risque de disparition de ces dernières du Canada. L'analyse est fondée sur le modèle de diffusion présenté dans Dennis et coll. (1991). Ce modèle présente une projection des populations le long d'une trajectoire établie selon des tendances récentes, dont les variations sont attribuables à la variabilité naturelle. La population d'otaries à fourrure du Pacifique Nord était considérée comme une métapopulation, et chaque aire de reproduction représentait une sous-population (la plus petite aire de reproduction située à l'île San Miguel a été exclue de l'analyse). Les tendances récentes relatives à chacune des sous-populations ont été estimées à partir du nombre de petits en utilisant des modèles qui dépendent ou non de la densité. On a supposé que la variation inexpliquée représentait la variabilité naturelle (stochasticité démographique ou variabilité environnementale) après avoir fait les ajustements nécéssaires pour les erreurs de mesure. Les modèles ont été adaptés aux plus récentes séries chronologiques du nombre de petits qui étaient échelonnées sur 10 ans, 30 ans et 50 ans. Les techniques de Monte Carlo ont été utilisées pour projeter l'évolution de chacune des sous-populations 200 ans dans l'avenir, et pour estimer le risque de quasi-extinction au cours des 100 premières années de la projection. Le seuil de quasi-extinction a été fixé à 1 000 individus pour maintenir la diversité génétique, ce qui correspond à la taille effective de la population. Pour une espèce polygame comme l'otarie à fourrure du Nord, cela représente une sous-population totale de 8 000 otaries. J'ai adopté une approche de précaution. J'ai ainsi déterminé que les sous-populations seraient en voie de disparition s'il y avait 1 % de risque que la taille de ces dernières atteigne les niveaux de quasi-extinction au cours des 100 prochaines années, et j'ai déterminé que les sous-populations seraient menacées s'il y avait 20 % de risque qu'elles deviennent des espèces en voie de disparition au cours des 20 prochaines années. Les données de marquage ont été analysées afin de déterminer la contribution de chaque sous-population à l'abondance d'otaries à fourrure du Nord au Canada en fonction de la tendance qu'ont les animaux de chaque aire de reproduction à migrer le long de la côte Ouest de l'Amérique du Nord. Le seuil de quasi-extinction de la population et de la portion d'otaries qui migrent dans les eaux canadiennes a été fixé à 7 000 adultes ou 10 000 otaries, ce qui correspond à la taille minimale d'une population viable. L'analyse de la viabilité de la population a révélé que toutes les sous-populations sont actuellement sans danger, car il y a peu de risques (entre 0,00 % et 0,42 %) qu'elles disparaissent au cours du prochain siècle. La taille de la sous-population des îles Pribilof, où se trouve la plus grande aire de reproduction et d'où provient la majorité des otaries qui migrent dans les eaux canadiennes, a diminué au cours des 50 dernières années. Cependant, en raison de sa grande taille, la sous-population ne risque pas de disparaître au cours des 100 prochaines années, mais la probabilité de quasi-extinction s'intensifiera si elle continue de diminuer après le prochain siècle. Comme la sous-population des îles Pribilof diminue, les otaries provenant d'autres aires de reproduction où le nombre d'individus est stable ou a augmenté joueront un rôle de plus en plus important pour maintenir une population minimale viable au Canada. Par ailleurs, il ne semble pas y avoir de risque visible que les otaries disparaissent des eaux canadiennes. À l'heure actuelle, on estime que 75 % des otaries qui migrent dans les eaux canadiennes proviennent des îles Pribilof, alors que ce pourcentage s'élevait à 97 % lorsque des données ont été recueillies dans le cadre des recherches sur les poissons pélagiques effectuées de 1958 à 1974. Environ 15 % des otaries du Canada proviennent de l'aire de reproduction en constante croissance qui a été établie sur l'île Bogoslof en 1980, et 8 % des otaries proviennent des îles du Commandeur, où la taille de la sous-population a augmenté au cours des 50 dernières années, mais est maintenant devenue stable. Moins de 1 % des otaries proviennent des aires de reproduction éloignées situées sur les îles des Kouriles et l'île Tuleny (Tyuleniy), qui connaissent une certaine croissance. L'évaluation indique que le risque de disparition est une fonction de la taille de la population, de la tendance et du degré de variabilité naturelle, et que l'analyse de la viabilité de la population permet d'intégrer ces renseignements. La tendance d'une population ne constitue toutefois pas un critère utile pour évaluer les risques, en particulier les risques encourus par une très grande population comme les otaries à fourrure du Nord. En effet, on s'attend à ce que l'otarie à fourrure du Nord continue d'être le pinnipède le plus abondant et répandu du Pacifique Nord.

# INTRODUCTION

In 2003 the Government of Canada implemented the Species at Risk Act to protect species that were at risk of extirpation. The legislation provides for enhanced protection measures, such as development of recovery plans and designation of critical habitat, for endangered species facing imminent extirpation or extinction from Canadian waters, and for threatened species that are likely to become endangered species if nothing is done to reverse the factors leading to extirpation or extinction. SARA thus compliments the Fisheries and Oceans Acts that provide broader protection to conserve marine resources, habitat and ecosystems in Canada.

Assessing the risk of extirpation or extinction of a species is not an easy or straightforward task. Conservation biology has been focused on two key paradigms: the small-population paradigm that deals with the effects of smallness on the persistence of a population, and the declining population that focuses on the cause of smallness and its cure (Caughley 1994). It is generally recognized that the risk of extinction is low for large or stable populations, but high for small or declining populations. Small, declining populations face the greatest at risk, whereas large, stable populations face the least risk of extinction. In lieu of direct measures of the risk of extinction, various listing criteria have been developed based on the size (number of individuals, geographic range) or the trend (rate of decline) of populations (IUCN 1994; COSEWIC 2010a).

In practice, generic guidelines based on population size and trend may not apply across all taxa or species. The population-size – population-trend paradigm is particularly problematic for a species like the northern fur seal (*Callorhinus ursinus*). Northern fur seals have undergone a dramatic shift in distribution in recent decades. Pup production has been steadily declining at the largest breeding site on the Pribilof Islands, and historically the source of most animals migrating though Canadian waters. However, other breeding sites have been stable or increasing, and several new but small breeding sites have been established. Despite the recent declines on the Pribilof Islands, the species is still the most abundant and widely distributed pinniped in the North Pacific Ocean, outnumbering all other species combined (Olesiuk 2007). Application of SARA to such an abundant and widespread species would set a new precedent.

Population viability analyses (PVA) is a modelling technique developed to quantify the risk of extinction (Beissinger and McCullough 2002). There are various approaches to PVA, but they all attempt to project population trends into the future based on the current population status and recent trends and/or perceived threats. The projections account for both the trajectory (trend) of the population, as well as variability from the underlying trajectory due to demographic or environmental stochasticity. The projections are used to estimated the likelihood of the population becoming extinct or falling below a quasi-extinction threshold. Thus, PVA is a useful tool for integrating information on population size, trend and natural variability.

In this report, I develop a PVA to assess the risk of extirpation of northern fur seals in Canadian waters. Fur seals in the North Pacific were considered to be a meta-population, with each main breeding site representing a separate subpopulation. The PVA projects future trajectories for each breeding subpopulation based on the most recent pup count, recent trends in pup production, and variability in pup production at each breeding site, and thus integrates information on population size and trend. I estimate the effective population size that would be required to maintain genetic diversity of a fur seal subpopulation based on the polygamous breeding behaviour in this species. Projections were conducted to determine the risk of each subpopulation falling below the effective population size (risk of quasi-extinction). Finally, migration patterns were examined using tagging data to assess the influence of each breeding subpopulation on the abundance and viability of fur seals utilizing Canadian waters.

# DEVELOPMENT OF PVA MODEL

## OVERVIEW

The fur seal PVA consists of 3 steps: 1) fitting trajectories to the recent time-series of fur seal pup counts at each breeding site; 2) projecting the trajectories into the future to asses the risk of quasi-extinction for each breeding site; and 3) estimating the overall abundance of fur seals in Canadian waters based on the projections for each subpopulation and the propensity of animals from each breeding site to winter along the west coast of North America (WCNA) and in Canadian waters.

The reason(s) for the decline in pup production on the Pribilof Islands are unknown, but human-induced mortality appears to be negligible (DFO 2008; Allen and Angliss 2011). The northern fur seal has been the subject of comprehensive population studies and extensive demographic data, life tables and population models are available (York and Hartey 1981; Trites 1984[1], 1989; Trites and Larkin 1989; Eberhardt 1990; Smith and Polachek 1981; see reviews by York 1987 and Ragen and Fowler 1992). However, the demographic data are somewhat antiquated and not useful for assessing the extent to which recent declines in productivity are due to increases in mortality, declines in birth rate, or emigration to other breeding sites. I therefore adopted a simple diffusion model (Dennis et al. 1991) that projected total population size based on pup counts.

## POPULATION UNIT

The northern fur seal is endemic to the North Pacific Ocean. The genus is represented by a single species and no subspecies are recognized (Taylor et al. 1955; Scheffer 1958; Rice 1998). Northern fur seals breed at six main sites: 1) Pribilof Islands; 2) Commander Islands; 3) Kuril Islands; Tyuleniy (Robben) Island; 4) Bogoslof Island; and 5) San Miguel Island (Figure 1). Animals tend to return to their natal birth site to reproduce, but there is also considerable exchange of both males and females among breeding sites (Lander and Kajimura 1982; Pinsky et al. 2010), and as a result no evidence of genetic differentiation among breeding sites (Rice 1998; Ream 2002). Outside the breeding season, fur seal are pelagic and widely distributed throughout the North Pacific Ocean (Figure 1), and there is considerable intermixing of subpopulations during the pelagic migration (Taylor et al. 1955; NPFSC 1962, 1969, 1971, 1975; Lander and Kajimura 1982).

SARA defines a species that can be designated as including a species, subspecies, variety or geographically or genetically distinct populations of animal, but provides little guidance on defining distinctness. With respect to geographic distinctness, COSEWIC (2010) guidelines allow for the designation of units separated by major range disjunction, defined as disjunction between substantial portions of the species' global geographic range such that dispersal of individuals between separated regions has been severely limited for an extended period of time and is not likely in the foreseeable future. With respect to genetic distinctness, COSEWIC (2010) guidelines allow for designation of units showing evidence of genetic distinctiveness including, but not limited to, appropriate inherited traits (morphological, life history, behaviour) and/or genetic markers. Given the broad and continuous distribution of fur seals across the North Pacific Ocean, extensive inter-mixing, and lack of genetic differentiation, northern fur seals are regarded as comprising a single population (DFO 2008; Olesiuk 2007; COSEWIC 2011).

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

For the PVA, I considered the fur seals to comprise a meta-population, with each of the 6 breeding sites considered to be subpopulations.  While there may be sufficient exchange of individuals among breeding sites and inter-mixing at sea to preclude listing of individual subpopulations, it nevertheless needs to be recognized that the subpopulations differ in size and proximity to the Canadian portion of their range, and thus have varying influence on the status of fur seals in Canada.  In particular, the largest breeding subpopulation on the Pribilof Islands and source of most of the animals in Canada has been declining, whereas the smaller, more distant subpopulations have been stable or increasing.  The pertinent question is whether the declines on the Pribilof Islands put the species at risk in Canada, or whether there is sufficient influx of animals from other subpopulations to maintain viable numbers in Canada.

## PVA MODEL

The fur seal PVA is based on the diffusion model developed by Dennis et al. (1991) that projects a population into the future based on recent population trends (trajectory) and the degree of variability from the underlying trajectory (stochasticity).  The diffusion model is a simplification of models based on Leslie (1945) projection matrices specifying sex- and age-specific fecundity and survival rates.  Up-to-date data on annual reproductive and survival rates are not available for northern fur seals.  However, when demographic parameters are stable or change slowly over time, the population will develop a stable sex- and age-structure in which the relative proportions of sex- and age-class remains fairly constant.  Under these conditions the population is said to be stationary, and its trajectory can be described in terms of total abundance or any component of the population.

In its simplest form where the rate of population change is constant (no density dependence):

[1]    $N_t = N_0 \cdot \lambda^t$

where $N_0$ and $N_t$ denote the initial population size and size at time $t$ respectively, and $\lambda$ the annual finite rate of increase (or dominant eigenvalue of the Leslie matrix).

To test for density dependence, I also fitted the generalized logistic equation, which allows for the rate of increase to slow with increasing density:

[2]    $N_{t+1} = N_t + N_t \cdot \lambda \, [1-(Nt/K)\theta)]$

where $K$ represents the carrying capacity and $\theta$ a shape parameter indicating how abruptly the rate of increase slows with density.

In projecting the trend forward through time, the Dennis et al. (1991) model assumes that $ln(Nt)$ changes over time as a Weiner process that drifts with mean $r$ (trajectory) and variance $\sigma^2$ (stochasticity), where $r=ln(\lambda)$ represents the intrinsic rate of increase.  Dennis et al. (1991) outline methods for estimating the parameters from survey counts using regression techniques, and provide formulae for calculating time to extinction.  Monte Carlo techniques can also be used to project populations into the future, with each realization:

[3]    $ln(Nt) = ln(N_0) + \sum x_i$                    for $i=1,\ldots,t$

where $x_i \sim$ Normal $(r,\sigma^2)$. Thus, the future of the population and risk of extinction is a function of its initial size, $N_0$, the rate of change over time, $\lambda$, and the degree of stochasticity, $\sigma$ (Figure 2).

## RECENT TRENDS

Northern fur seal assessments are based on counts of pups at rookeries, the only segment of the population that is ashore at any given time that can be enumerated (Berkson and DeMaster 1985). Pup production (live and dead pups) has been estimated at all major rookeries, usually on an annual or biennial basis (Figure 3). For U.S. sites, counts, estimates of precision and a description of methods were obtained from the annual Fur Seal Investigation Reports (Lander 1980a; Kozloff 1982, 1985, 1986; Kozloff and Kajimura 1986; Kajimura 1990a, 1990b; Kajimura and Sinclair 1992; Sinclair 1993, 1994a, 1994b, 1996, 1997a, 1997b; Sinclair and Robson 1999; Robson 2000, 2001, 2002; Testa 2005, 2007, 2008; see review by York 2005a). For Russian sites, counts were obtained from Lander (1980a), Burkanov and Calkins (2007), Burkanov et al. (2007), and Kuzin (2010).

For a number of reasons, I considered pup counts to be an good metric for the PVA. Since each female gives birth to a single offspring, pup production provides an indirect measure of the number of reproductive females. Moreover, females appear to limit productivity of fur seal populations, and past collapses of the fur seal population have been associated with harvesting of females (Scheffer et al. 1984; Fowler 1997; Gentry 1998). In contrast, the population has recovered during periods of harvesting of males (Gentry 1998; Kuzin 2010). Finally, fur seals wintering along WCNA are predominately adult females, so pup counts are also relevant for assessing status of fur seals in Canadian waters.

It is unclear what time-frame should be used for assessing recent trends. Longer time-series capture more of the history of population changes, but conditions and growth rates are more likely to vary over longer periods. Shorter time-series reflect the most recent trends, but are subject to bias due to fluctuations and measurement error. For the fur seal PVA, I fitted trends to the most recent 10-year, 30-year and 50-year time series of pup counts. A 10-year period is the minimum time span advocated by COSEWIC (2010) for assessments, and since counts were often made biennially it was the shortest time-series for which statistically meaningful trends could be estimated. The 30-year period represents 3 generations for fur seals, and is the time frame recommended by COSEWIC (2010). The 50-year time period was roughly the time frame used in several Steller sea lion PVAs (Gerber and VanBlaricom 2001; Goodman 2006; NMFS 2008), and it also roughly coincides with the onset of the recent declines on the Pribilof Islands. Longer time-series were not considered, as the fur seal population was still recovering from pelagic sealing that has depleted numbers in the late 1800s and early 1900s.

The San Miguel subpopulation is somewhat unique from several perspectives, and I excluded it from the PVA analysis. First it is the smallest breeding subpopulation, and thus has the least influence on overall viability of the population. Second, it is the only breeding site at lower latitudes, and although satellite telemetry data indicate the animals utilize Canadian waters (R. DeLong and J. Sterling, National Marine Mammal Laboratory, Seattle, WA, pers. comm.), detailed descriptions of migration patterns have not been published. Third, pup production on San Miguel Island has exhibited marked fluctuations related to *El Nino* events (DeLong and Antonelis 1991; Melin et al. 2005). The fairly rapid recovery from these events suggests pup survival is impacted to a greater degree than older age-classes. As a result, the sex- and age-structure of the San Miguel subpopulation is not likely to be stationary, and the diffusion model inappropriate for projecting trends.

## MEASUREMENT ERROR AND NATURAL VARIATION

The diffusion model assumes $\sigma$ is due to natural variation, $\sigma_{NV}$. The regression techniques developed by Dennis et al. (1991) provide a measure of total variation from the underlying growth trajectory, the mean squared error (MSE), which overestimates $\sigma_{NV}$ if there is also measurement

error, $\sigma_{ME}$, associated with the survey counts. Assuming that $\sigma_{ME}$ and $\sigma_{NV}$ are independent, an unbiased estimate of $\sigma_{NV}$ can be obtained from:

[4] $\qquad \sigma_{NV}^2 = MSE - \sigma_{ME}^2$

The Annual Fur Seal Investigation Reports generally provided estimates of the SE associated with each pup count. Given a time-series of survey counts, $N_t$ over time $t=1,\ldots,k$, an estimate of measurement variance can be obtained by:

[5] $\qquad \sigma_{ME}^2 = \dfrac{1}{k} \sum_1^k \left[ \dfrac{S_t^2}{n_t \cdot \overline{N}_t^2} + \dfrac{S_{t+1}^2}{n_{t+1} \cdot \overline{N}_{t+1}^2} \right]$ $\qquad$ Morris and Doak (2002)

where $S_t^2$ is the sampling variance associated with the $t$th count, $n_t$ the number of replicates for the $t$th count, and $N_t^2$ the mean of the counts in the $t$th year.

Except for the most recent counts on the Kuril Islands (Burkanov and Calkins 2007), the precision of pup counts on Russian rookeries was not reported. I thus ignored measurement error, and assumed all deviations from the underlying trajectory were attributed to natural variability. This overestimates the degree of stochasticity and risk of extinction, but as will be shown the Russian sites were all large and stable or increasing, so this had no effect on the overall conclusions.

It should be noted that pup numbers are probably more variable than total population size or number of reproductive females, due to inter-annual variations in pregnancy rates (Trites and York 1993). This would overestimate the natural variability at a population level, but this was not considered to be a serious problem as pup counts exhibited modest year-to-year variability. However, this would be a more important problem for the San Miguel Island subpopulation, where there is much greater inter-annual variability in pup production associated with *El Nino* years. Pup counts decline abruptly during *El Nino* events, but judging from the rapid recovery in subsequent years it appears that high mortality is somewhat buffered in adult females (DeLong and Antonelis 1991; Melin et al. 2005).

**PROJECTIONS**

To assess risk of extirpation, the 5 subpopulations were each projected 200 years into the future. I used Monte Carlo sampling with 10,000 replicates to assess the effects of natural variability. For the Pribilof Islands, pup counts on St. Paul and St. George Islands were made separately and not always in the same year, so they were projected separately and the results combined to assess risk of extirpation.

Each realization of the projection is given by:

[6] $\qquad ln(N_{jt}) = ln(N_{j0}) + \sum x_i$

where $N_{j0}$ denotes the most recent pup count for the $j$th subpopulation, $N_{jt}$ the projected pup count for the $j$th subpopulation in year $t$, and $x_i$ is a series of 200 normally distributed random variates with mean, $r_j$, and $\sigma_j^2$ (the intrinsic growth rate and associated variance for the $j$th subpopulation). The first 20 years of the projection was used to assess the probability of the subpopulation falling to levels it would be considered threatened, and the first 100 years the risk of attaining one of the quasi-extinction thresholds.

The effects of imposing constraints on the simulated values were also examined. Some of the models indicated increasing trends with no evidence of density-dependence, so pup production was constrained from escalating to unrealistic levels. For the least conservative upper limit, the number of pups in the realization was limited to the maximum number that had ever been counted at the site over its history. This would be reasonable if pup production was limited by available habitat, and no habitat loss had occurred. As a more conservative upper limit, the number of pups in the realization was limited to the maximum pup count in the time-series to which the trajectory had been fitted. This essentially assumes that all subpopulations were at their current carrying capacity and the model did not allow for any further growth. I also examined annual growth rates to determine if they were realistic. The largest rates of increase (up to 46%) were observed on Bogoslof Island as it was being colonized, during which period the growth was obviously being supported by immigration from other subpopulations (Loughlin and Miller 1989; Ream et al. 1999). Estimated rates of increase ranged from -0.027 to +0.032 for the remaining subpopulations and were considered to be realistic.

There was no history by which to measure carrying capacity of Bogoslof Island, which arose from the Pacific Ocean in 1890. The subpopulation has exhibited dramatic growth since it was colonized by fur seals in 1980. However, Bogoslof is a small island, and space somewhat limited, and although there appears to be room for further expansion the surrounding prey resources may be limiting growth (T. Gelatt and R. Ream, National Marine Mammal Laboratory, Seattle, WA, pers. comm..). As a conservative upper limit, I set the upper limit to the most recent pup count of 22,905 in 2011 (Towell and Ream 2012), which assumes that no furthern growth will occur. The Kuril Island subpopulation has exhibited steady growth since being repopulated in 1955-56 (Burkanov and Calkins 2007). I am not aware of any historical estimates of abundance prior to the large kills in the 1800s that extirpated the site, so again the upper limit was conservatively set as the most recent and highest pup count of 30,192 in 2005 (Burkanov and Calkins 2007).

**EXTINCTION THRESHOLD**

PVA models involving meta-populations have often assessed the risk of extinction based on the proportion of subpopulations that decline to zero or near zero levels. For example, both York et al. (1996) and Winship and Trites (2006) considered each of the 33 rookeries in the western population of Steller sea lions to be subpopulations, and concluded that the overall population was at little risk of extirpation within the next 100 years, but that many of the subpopulations would likely disappear if the population declines in the population declines observed during the 1990s were to continue. Given the limited number of fur seal subpopulations and their important role in providing immigrants for re-populating or establishing new breeding sites, the conservation goal should be to maintain a viable population with multiple viable subpopulations. I thus assessed the risk of extinction at both the population and subpopulation level.

The dynamics of severely depleted populations on the verge of extinction are difficult to predict. Demographic stochasticity and natural variability plays an increasing predominant role when as abundance falls to very low levels, and their may be adverse depensatory or Allee affects at very low densities (Gerber and Hilborn 2001; Beissinger and McCullough 2002). Although the largest rates of increase for fur seals have been observed in sites being (re)colonized, these increases were driven largely my immigration from other, larger subpopulations. It is thus not possible to assess the adverse effects that might occur at low densities were there not healthy subpopulations available to seed them, although Gerber and Hilborn (2001) noted a number of examples where otariid populations had recovered from very low levels.

Given the difficulties in modelling populations at very low densities, its common to set some higher, more conservative, quasi-extinction threshold. One of the main concerns for small

populations is the loss of genetic diversity.  Genetic diversity is a function of the effective population size, $N_e$, which represents the number of individuals contributing genes to the next generation (Wright 1931).  As a general rule, an $N_e$ of 50 adults avoids inbreeding depression in the short-term; an $N_e$ of 500 is required to avoid serious long-term genetic drift; and an $N_e$ of 1,000 provides a conservative estimate beyond which significant additional genetic variation is not expected (Allendorf and Ryman 2002).  I thus adopted an $N_e$ of 1,000 as a conservative threshold for quasi- extinction for each fur seal subpopulation.

The effective population size only includes only breeding animals, and is thus smaller than the total population size (Waples 2002).  The number of breeding animals varies as a function of the mating system.  For polygamous species like northern fur seal, the calculation has to account for the fact that many males do not mate, and can estimated by:

[7]     $N_e = 4 \cdot N_{ef} \cdot N_{em} / N_{ef} + N_{em}$

where $N_{ef}$ and $N_{em}$ denote the number of adult females and males respectively (Wright 1931).  Fur seals are polygamous with a harem mating structure where males compete for groups of females at the beginning of each breeding season and a successful male mates with all of the female groups in his group (Chepko-Sade et al. 1987).  In such cases, Nomura (2002) argued that, in order to account for variability in mating success, a more appropriate formula is:

[8]     $N_e = 4 \cdot N_{ef} \cdot N_{em} / N_{ef} + 2 \cdot N_{em}$

As can be seen from equations [7] and [8], in both cases the $N_e$ diminishes with increasing sex ratios, termed the harem effect.  However, the difference is very small as harem sizes increase (about 3% for harem size of 31.3 for fur seals; see below).

Equations [7] and [8] both refer to a single cohort.  Where generations of reproductive animals overlap, as is the case for northern fur seals, the effects of increasing harem size diminishes with increasing longevity.  Nunney (1993) showed that for harem polygyny in which females mate with only one male per breeding season, and form groups of size, $h$, the effective population size can be estimated as:.

[9]     $N_e = 2 \cdot N / 2(SV_m + SV_f) + (1 - SV_f)(h + 1)$

where $SV_f$ and $SV_m$ denote the proportion of reproductive females and males that survive to the next breeding season.  Note that if we set $SV_f = SV_m = 0$ as would be the case for non-overlapping generations, equations [9] and [7] are equivalent, so I applied an adjustment of 3% to equation [9] to account for variability in mating success.  Based on life tables for female northern fur seals (Lander 1981; York and Hartley 1981; Loughlin et al. 1994; York 2005; Olesiuk 2007), the mean weighted survival rate of adult females was estimated to be about 0.93.   Data is more limited for breeding males, but based on a sample of territorial bulls collected by Johnson (1955), mean weighted survival was estimated to be about 0.55 (Lander 1981; Olesiuk 2007).  NMFS surveys on the Pribilof Islands include counts of males on rookeries, and the ratio of pups (assumed to be equivalent to the number of reproductive females) to territorial (Class 3) bulls.  Since 1980 (the post-harvesting period) the ratio has averaged about 31:1.  Substituting these values into Equation [9] indicates that the effective population size for northern fur seals would be about 28% of the adult population size.  Based on life tables (Lander 1981; York and Hartley 1981; Loughlin et al. 1994; York 2005; Olesiuk 2007), an $N_e$ of 1,000 (3,570 adults) equates to total population size of 8,100 animals or 1,800 pups.  These estimate are probably somewhat high in that some mating may occur by non-territorial bulls on the periphery of the rookery.  The estimate of $N_e$ for fur seals is somewhat higher than Goodman's (2008) estimate that a total population of 4,532 Steller sea lions would be required to maintain a $N_e$ of 1,000, but he did not provide details on

how the value was calculated.  The estimate that $N_e$ is 28% of adult fur seal population is intermediate to the estimates of 15% and 37% for South American fur seals in an *El Nino* and normal year respectively (Rosa de Oliveria et al. 2006).

A second, more conservative measure of secure population levels is the minimum viable population (MVP), defined as the smallest size required for a population or species to have a predetermined probability of persistence for a given length time (Shaffer 1981).  MVP calculations generally consider the combined effects of age-structure, demographic stochasticity, environmental variability, and inbreeding depression (McCarthy et al. 2001).  Reed et al. (2003) reviewed MVPs across a wide range of taxa, including several species of marine mammals, and concluded that a MVP of about 7,000 adults would typically be required to assure a 99% probability of persistence over 40 generations.  For fur seals, this equates to a total population size of about 16,000 animals.

It is unclear what threshold level should be adopted for assessing the status of fur seals within Canadian waters.  The species only occurs seasonally (Bigg 1990), there are no breeding sites in Canada and, because of the segregation that occurs during the pelagic migration, adult males are poorly represented.  In reality, the concept of viability within Canada is difficult to assess outside the context of the full range of this highly-migratory, trans-boundary population.  For lack of better criteria, I assumed that if the entire fur seal population was not at risk, and none of the subpopulations were at risk, and that if numbers migrating through Canadian waters were maintained at levels in excess of required to sustain a minimum viable population (MVP), that fur seals in Canada were not at risk of extirpation.

There is obviously a great deal of uncertainty associated with projecting the probability of quasi-extinction far into the future, and an acceptable level of risk and an appropriate time-frame need to be considered.  SARA defines an endangered species as one that is facing imminent extirpation or extinction, and a threatened species as one that is likely to become endangered if nothing is done to reverse the factors leading to its extirpation or extinction, but provides no guidance in interpreting the definitions. COSEWIC (2010) and IUCN (2004) guidelines suggest a 20% probability of extinction within 20 years or 5 generations, whichever is longer, up to a maximum of 100 years, as the threshold for threatened, and a 10% probability of extinction within 100 years as the threshold for endangered.  Gerber and DeMaster (1999) recognized the practical limitations of long-term forecasts for management, and advocated a shorter time period, and considered a species to be endangered if the chance of extinction within 10 years was greater than 5%, and threatened if the population fell below quasi-extinction levels within 30 years.  Recognizing the uncertainty in deriving estimates of quasi-extinction, Angliss et al. (2002) advocated a more precautionary approach for large whales, and considered a species to be endangered if there was a 1% chance of quasi-extinction within 100 years, and threatened if there was a 20% chance of the population becoming endangered in the next 20 years.  Being the most conservative, I adopted the Angliss et al. (2002) criteria for the northern fur seal PVA.

**MIGRATION PATTERNS**

Fur seals tend to return to their natal birth site to reproduce (DeLong 1982; Baker et al. 1995; Gentry 1998), but there is also considerable exchange of animals among breeding sites  (NPFSC 1961, 1964, 1967, 1974; Lander and Kajimura 1982; Pinsky et al. 2010).  Fur seals become widely distributed throughout the North Pacific during their pelagic migration (Bigg 1990; Olesiuk 2007, 2012) (Figure 1), and there is also extensive inter-mixing among subpopulations at sea (NPFSC 1961, 1964, 1967 1974).  Nevertheless, the species is not panmictic. Fur seals breeding on Russian rookeries in the Sea of Okhotsk tend to winter along the Asian coast, whereas fur seals breeding on U.S. rookeries in the Bering sea tend to winter along the west coast of North America (WCNA) (NPFSC 1961, 1964, 1967, 1974; Lander and Kajimura 1982).  Migrating fur

seals also segregate by sex and age (Antonelis and Perez 1984; Bigg 1990).  Juveniles of both sexes go to sea shortly after weaning (Ragen et al. 1995), where they remain for the first 2-4 years of life and become widely distributed throughout the North Pacific (Bigg 1990; NMFS 2007; Olesiuk 2007, 2012).  Older males tend to winter at higher latitudes, and adult females tend to congregate in coastal areas (Antonelis and Perez 1984; Bigg 1990).  Thus, northern fur seals in Canada are only represented by a segment of population, and abundance in Canadian waters is influenced more by breeding sites in the Bering Sea and less by the more distant breeding sites in the Sea of Okhotsk.

Information on the origin of animals wintering along WCNA is provided by flipper-tag programs. Fur seals have been subject to some of the largest-scale tagging efforts, with over a million  pups tagged during research that included all major rookeries (York 2005b).  Large-scale tagging on U.S. rookeries (St. George and St. Paul Islands) began in 1941 and 1956 respectively, and continued until 1968, beyond which point pups were marked but not tagged.  Large-scale tagging on Russian rookeries (Medny and Berring Islands in the Commander Islands, and Tyuleniy Island) began in 1958 and continued into 1970s.  Since I was interested in the relative contribution of animals from both American and Russian rookeries, I restricted the analyses to the 1958 to 1968 cohorts when tagging was being conducted at all major rookeries.  A total of 609,742 tags, representing an average of 11.9% of pups born, were deployed during this period (Table 1).

A total of 208 tags were recovered off the WCNA from the 1958-1968 cohorts during the NPFSC pelagic research collections during 1958-74 (Table 2).  As expected, the vast majority of tags recovered off WCNA (94%) had been tagged on the Pribilof Islands.  However, the relative proportions of tags is dependent on various factors including the tagging effort at each breeding site, the number of pups born at each breeding site, and the propensity of animals from each breeding site to winter along the WCNA.

The proportion of seals originating from each of $j$ subpopulations, $Pr(adj)_j$, can be estimated by adjusting tag recoveries for differences in tagging rates among the $j$ sites and $t$ cohorts:

$$[10] \qquad Pr(adj)_{jt} = Pr_{jt} / NT_{jt} / NB_{jt}$$

where $Pr_{jt}$ denotes the unadjusted proportion of tags recovered from $j$th site for the $t$th cohort, and $NT_{jt}$ and $NB_{jt}$ denote the number of pups tagged and number of pups born at the $j$th site for the $t$th cohort.  The denominator in equation [10] represents the tagging rate (i.e. proportion of pups tagged), and is mathematically equivalent to the tables of reciprocals used by NPFSC (1964, 1967, 1971, 1975) to adjust for sampling effort prior to the advent of spreadsheets.  The adjusted proportions represent the relative number of tags that would have been recovered had sampling effort been the same at all sites.

The adjusted tag recoveries indicate that 97.5% of the fur seals wintering along WCNA during 1958-74 originated from the Pribilof Islands, 2.3% from the Commander Islands, and 0.2% from Tyuleniy Island (Table 3).  These proportions reflect the combined effects of the different sizes of each breeding site, as well as differences in the propensity of animals from each site to migrate along the WCNA.  The high proportion of animals from the Pribilof Islands can be attributed to the fact it was the largest subpopulation at the time, and it was also the closest breeding site so animals had a higher propensity to winter along WCNA.

For the PVA, I was interested in the assessing the relative contribution of each breeding site to the population of seals wintering along WCNA and in Canadian waters, which will vary as the sites have different trajectories.  We can obtain an estimate of the relative propensity of seals

from each site to winter along WCNA, *Pr(WCNA)$_{jt}$*, by adjusting for the differences in the size of sites when tagging occurred:

$$[11] \quad Pr(WCNA)_{jt} \; \alpha \; Pr(adj)_{jt} / NB_{jt}$$

where *NB$_{ij}$* has already been defined as the number of pups born. Just as the recoveries had been adjusted for tagging effort, equation [11] adjusts for the size of each site. The weighted mean *Pr(WCNA)$_j$* summed over all cohorts provides an estimate of the relative number of tags that would have been recovered from each site had they been equal in size (and tagging rates were the same). It thus provides a measure of the relative propensity of animals born on each site to winter along WCNA. Since only a segment of each subpopulation winters off WCNA, and since animals segregate by sex and age during the migration, it needs to be stressed these indices are only meaningful on a relative scale, so I arbitrarily scaled them such that the site exhibiting the greatest propensity to migrate along WCNA was set to 100%.

The analysis indicated that, as expected, animals born and tagged on the closest subpopulation at the Pribilof Islands had the highest propensity to winter along the WCNA, whereas animals born on the Commander Islands were only 20% as likely to winter off WCNA, and animals from the most distant subpopulation on Tyuleniy Island only 4% as likely as Pribilof Island animals to winter off WCNA.

A second, smaller sample of tag resightings was made on reproductive females as the new rookery at San Miguel Island was being colonized (Table 2). While less precise due to smaller sample sizes, these resights gave similar results, indicating that animals born on the Pribilof Islands exhibited the greatest propensity to breed on San Miguel Island, whereas females born on the more distant sites on the Commander Islands and Tyuleniy Island were only 20% and 3% as likely to breed on San Miguel Island. Given the similarity of the NPFSC pelagic tag recoveries and San Miguel tag resights, the two datasets were combined, which indicated that animals born on the Commander Islands and Tyuleniy Island were 20% and 3% as likely to occur off WCNA as animals from the Pribilof Islands.

The propensity of animals from the various subpopulations to winter on WCNA appears to be inversely related to distance. This pattern was also evident from an analogous analysis of tags recovered off Japan (1,125 tags from 20,107 collected specimens). Tag recoveries, when corrected for tagging effort, indicated that 61% of the animals collected off Japan were born on Tyuleniy Island, the closest breeding site, 22% from the Commander Islands, 16% from the Pribilof Islands, and 1% from the Kuril Islands. When adjusted for the size of each breeding site, the data showed that animals from Tyuleniy Island, the closest breeding site, had the highest propensity to winter in coastal waters off Japan, whereas animals from the Commander Islands, the next closest site, were only 33% as likely to winter off Japan and animals from the Pribilof Islands, the most distant site, only as 3% as likely to winter off Japan. Thus, the high prevalence of Pribilof Island animals off Japan was not due to their propensity to migrate to that area, but rather reflects the dominant size of the Pribilof Island subpopulation during that period. Unfortunately, I did not have access to the pelagic data or tag recoveries made by the USSR to complete the picture, but the scanty data I was able to glean from NPFSC (1975) indicated that most of the tagged animals recovered in the western Bering Sea were from the Commander Islands (11 of 13 tags), with a few from the Pribilof Islands (2 of 13 tags).

The relative migration propensities provides a method for weighting the relative contribution of each subpopulation to assess overall trends along WCNA and in Canadian waters. To illustrate this approach, I recalculated the proportion of animals from each breeding site based on the most recent pup counts (Table 4). For the new rookeries on the Kuril Islands and on Bogoslof Island, where tagging data for estimating migration propensities was not available, it was assumed

migration patterns were a function of distance.  The Pribilof Island value was applied to Bogoslof Island, as it is situated near the main migration corridor been the Pribilof Islands and Unimak Pass (Ragen et al. 1995).  For the Kuril Islands, I assumed the migration propensity was the same as the most distant site on Tyuleniy Island, such that it had relatively little affect on the WCNA or Canadian abundance.  The calculations indicate that animals born on the Pribilof Islands still account for the majority (75%) of the fur seals in Canadian waters, but not nearly to the same degree as during the 1958-74 pelagic collections.  Bogoslof Island and the Commander Islands, which have both grown in size, now account for significant numbers (15% and 8% respectively) of the fur seals in Canadian waters (Table 4).  When the 1958-68 cohorts were tagged, pup production on the Pribilof Islands was about 8X the pup production on the Commander Islands, and since Pribilof animals were 5X as likely to winter along WCNA, they outnumbered Commander Island animals by a factor of almost 40:1 (~3% from the Commander Islands).  However, with the recent declines on the Pribilof Islands and growth on the Commander Islands, pup production on the Pribilof Islands is now less than twice the pup production on the Commander Islands and, assuming migration patterns haven't changed, the ratio of animals off WCNA from these two sites is now on the order of 9:1.

## TOTAL ABUNDANCE

The sex- and age-segregation of animals during their pelagic migration needs to be considered when estimating the abundance of fur seals along WCNA.  Juveniles tend to be widely distributed across the North Pacific Ocean, and most males winter at higher latitudes, so they tend to be under-represented in coastal waters.  The migration pattern of females develops over their lifespan, with an increasing proportion older females congregating in coastal areas.  Antonelis and Perez (1984) developed a procedure for estimating fur seal abundance in the California Current ecosystem (California to Washington) based on the degree to which males and younger animals were under-represented in the NPFSC pelagic collections.  Based on their general knowledge of fur seal migration patterns, they estimated that 80% of females aged 5+ years wintered along the WCNA, and subsequently estimated the proportions of other sex- and age-classes based on the degree to which they were under-represented in the pelagic collections.  They estimated that 30% of immature seals and 10% of adult males wintered in California current ecosystem.  Olesiuk (2007) expanded their analysis to include coastal waters from California to SE Alaska (WCNA), and updated total abundance estimates based on pup production in 2006.  Based on the age-structure of females in the pelagic collections, Olesiuk (2007) assumed that migration patterns of females were fully developed by 8 years of age, and based on a small sample of satellite tracks of these older females, estimated that 75% (6 of 8; Ream et al. 2005; R. Ream, National Marine Mammal Laboratory, pers. comm.) of females aged 8+ years wintered along WCNA.  More recent satellite telemetry studies conducted by National Marine Mammal Laboratory's Alaska Ecosystems Program provide a larger sample, which indicated that 75% (27 of 36; J. Sterling, National Marine Mammal Laboratory, pers. comm.) of adult females with pups (assumed to represent females aged 5+ years) tagged on the Pribilof and Bogoslof Islands wintered along WCNA during peak seasonal abundance in March.  Based on the degree to which other sex- and age-classes were underrepresented in the pelagic collections (Olesiuk 2007), it was estimated that  27% of yearlings (56% female), 40% of juveniles aged 1-3 years, 75% of females aged 4+ years, and 9% of males aged 4+ years, which combined represent 52% of the total population, wintered in coastal waters along WCNA.  Assuming the Pribilof Islands subpopulation represented 97% of animals wintering off the WCNA, Olesiuk (2007) estimated that roughly 367,000 fur seals winter along WCNA.  Based on the relative densities of seals seen by area and month during the NPFSC sighting surveys, it was estimated that roughly 120,000 (34%) seals would inhabit Canadian waters during peak seasonal abundance in May (Olesiuk 2007).

Based on the relative migration propensities and most recent pup counts in 2005-2011, it was estimated that roughly 346,000 fur seals currently winter along WCNA, with something on the order of 118,000 passing through Canadian waters during peak seasonal abundance in May (Table 5). These are obviously crude estimates, but provide a benchmark by which to assess changes in abundance for the PVA.


# RESULTS


The Population Viability Analyses indicate that the 5 major breeding sites examined were all secure, and none face imminent extirpation. The main conservation focus for fur seals has been on the Pribilof Islands, where the once dominant herds have been declining since the mid-1950s (Figure 3a). The most parsimonious PVA models indicated the declines were density independent. Despite the protracted declines, there appears to be very little risk of extirpation in the foreseeable future (Table 6). Projections based on the most recent 50-year time-series of pup counts, over which the mean rate of decline was 1.8%, indicated there was only a 0.10% chance of the subpopulation falling to quasi-extinction levels ($N_e$<1,000 or $N$<8,000) within the next 100 years, and a 1.17% in next 120 years (Figure 4a). If the declines were to continue beyond the next century, mean time to extinction was estimated to be 161 years. Projections based on the most recent 30-year time-series of pup counts indicated a 0.12% and 1.45% chance of quasi-extinction within the next 100 and 120 years respectively, with mean time to extinction estimated to be 152 years. Projections based on the most recent 10-year time-series indicated a 0.29% and 2.07% chance of quasi-extinction within 100 and 120 years, and mean time to quasi-extinction was estimated to be 199 years. Projections for the 50-, 30 and 10-year time series of pup counts all indicate an escalating probability of quasi-extinction if the declines were to persist beyond the next century (Figure 5). Constraining growth to some upper limit had no discernible effect as the population was steadily declining.

The declines in pup production on the Pribilof Islands can be partly, but not fully, attributed to the dispersal of breeding animals to other subpopulations. The neighbouring rookery on Bogoslof Island has exhibited very rapid growth since being colonized in 1980. The only model fitted was to the 30-year time-series, as just three pup censuses had been conducted in the last decade. The most parsimonious model indicated the growth was density dependent and slowed as numbers increased. However the model fit poorly, with an MSE an order of magnitude greater than most other models (Table 6), and $\theta$ and $K$ of the generalized logistic poorly defined. Since the pup counts were complete tallies, it was assumed measurement error was negligible. The large degree of natural variability is likely attributable to stochastic effects in this small subpopulation. Although the population growth rate has slowed in recent years (from 46% to 15%), it is still far in excess of the maximum rate of increase for the species. The increases thus represent immigration from other sites, presumably largely from the neighbouring Pribilof Islands (Loughlin and Miller 1989; Ream et al. 1999). Due to its rapid growth, there was no discernible chance of the subpopulation reaching quasi-extinction levels in the next 100 and 120 years.

The Commander Island subpopulation increased dramatically during the first half of the 20th century as it recovered from pelagic sealing, peaking in the mid-1970s, but numbers have been relatively stable since then (Burkanov and Calkins 2007). None of the time-series exhibited evidence of density dependence. The projections indicated there was very little risk of extirpation for this subpopulation. For the 50-year series, none of the projections fell below the quasi-extinction threshold. For the 30-year time series, the chance of falling below the quasi – extinction threshold was 0.00% and 0.03% in 100 and 120 years respectively, and mean time to extinction was estimated to be 583 years. For the 10-year time series, the changes were 0.42% and 0.84% of quasi-extinction in 100 and 120 years respectively, with mean time to extinction estimated to be 485 years.

The Kuril Island subpopulation has increased, albeit somewhat sporadically, since the breeding site was re-populated in the 1950's. (Burkanov et al. 2007). Despite the growth, a few of the projections fell below the quasi-extinction threshold due to the high variability of counts (Table 5) and a lack of an estimate of their precision to adjust for measurement error. For the 50-year time series, there was a 0.79% and 1.05% chance of quasi-extinction within the next 100 and 120 years, but estimated mean time to extinction was in the tens of thousands of years. There were no cases of the subpopulation falling to quasi-extinction for the 30-year projection, and too few data to fit a 10-year time series.

Finally, the Tyuleniy Island subpopulation has shown no net change in pup production over the last 50 years. However, numbers were depleted as a result of over-harvesting prior to the early 1990s, but the subpopulation has since recovered (Kuzin 2010). The projection based on the 50-year time series, which included the periods of over-harvesting and subsequent recovery, indicated there was a 0.03% chance of quasi-extinction within 100 years, 0.05% chance within 120 years, and mean time to extinction was estimated to be 478 years. For projections based on the 30-year and 10-year time series, which represented the recovery period, there were no instances of abundance falling to quasi-extinction levels.

Although none of the subpopulations were deemed to be at risk of extirpation, their trajectories were quite different. Weighting the projections for each subpopulation by the propensity of animals to winter along WCNA, none of the realizations based on 10-year time-series indicated that abundance of animals migrating through Canadian waters would fall below MVP levels ($N$<7,000 adults). Indeed, even the most conservative projections, which capped pup production at all sites at recently observed levels (i.e. allowed for declines but no further growth), it was projected that no less than 33,000 seals or 23,000 adult seals will continue to pass through Canadian waters during the next century. Only 1% of projections indicated numbers falling below 17,400 seals or 12,200 adults over the next 100 years. Similarly, projections based on the 30-year time-series indicated there was no chance of numbers falling below MVP, and over the next century its expected that at least 42,000 seals or 29,000 adults will migrate through Canadian waters, with only 1% of projections indicating numbers falling below 15,100 seals or 12,900 adults. The 50-year projections also indicated there was no chance of numbers falling below MVP, and it is projected that at least 50,000 seals or 35,000 adults will continue to migrate through Canadian waters, with only 1% of the projections falling below 27,100 seals or 19,000 adults. It should be stressed these are conservative estimates as subpopulations were constrained to the maximum pup production observed over the time-series used in the projections, so there was no potential for further growth on the sites that have been growing for several decades.

## DISCUSSION

The Population Viability Analyses indicates that fur seals in the North Pacific are not at risk of extinction. All of the major breeding sites appear to be secure, and the species is not at risk of extirpation from the Canadian portion of its range. The analyses reaffirm that the once dominant fur seal subpopulation on the Pribilof Islands continues to decline. Nevertheless, it still constitutes the largest breeding site for the species, and the rate of decline relatively modest, such that even if the declines were to persist there is little chance of extirpation within the next 100 years. Moreover, all other subpopulations are stable or increasing, and there appears to be sufficient inter-mixing at sea to insure viable numbers will be sustained in Canadian waters over the next century irrespective of the fate of the Pribilof Island herd.

I consider the fur seal PVA to be quite conservative. Although subpopulations on Bogoslof and the Kuril Islands have both exhibited rapid growth over the past few decades, there was no

historical information on carrying capacity, and pup production at these sites was capped at the peak levels observed in recent surveys to prevent unrealistic growth. Some of the declines that over the last 50 years can be attributed to human-induced mortality sources which have since been eliminated. The Tyuleniy Island subpopulation was over-harvested until the 1980s, and the early declines on the Pribilof Islands were the result of lingering effects of an experimental kill of 300,000 adult females during 1956-61. No attempt was made to adjust for these anthropogenic effects prior to projecting future trends. I adopted conservative thresholds for quasi-extinction. The estimate of effective population size assumed only territorial bulls mate, but there is probably some mating by peripheral bulls. Subpopulations were considered to be quasi-extinct if they ever fell below a conservative effective population size, when in reality genetic diversity would be compromised during prolonged periods of depression (Hedrick 2000).

The PVA was based on past trends, and given the lack of understanding of the causes of the declines, it is difficult to project trends even a few years into the future, let alone a century or more. The projections should not be regarded as predications, but rather realizations of what would occur in the future were the recent trends to persist. In this regard, the PVA is a useful tool for integrating information on population size, trend and natural variability to assess the risk of extinction. An important lesson to be gleaned from this exercise is that population size or population trend, by themselves, are poor criteria for making listing decisions. Clearly large populations can sustain modest declines for considerable periods without risk, whereas small populations can fall below quasi-extinction threshold levels quickly, and very small populations are more at risk due to stochastic processes.

I made no attempt to account for catastrophic events, as I was not aware of any large-scale kills, except for harvests, and trying to model unforeseen events would have merely been a hypothetical gaming exercise. Again, the PVA projections need to be viewed as realizations if and only if recent conditions and trends persist. In this regard, it will be important to continue to monitor population trends, especially if abundance continues to decline and subpopulations approach quasi-extinction thresholds.

The northern fur seal has been described as exhibiting extreme site fidelity (Baker et al. 1995; Gentry 1998), and I would argue that this has been taken out of context for assessing risk. It is true that the majority of individuals return to their natal birth site to breed, and often return to the same stretch of beach in consecutive years. However, there is clearly extensive mixing of animals at sea during the pelagic migration, and sufficient exchange of adult animals between breeding sites to preclude genetic differentiation. Indeed, northern fur seals truly function as a meta-population, with immigrants from existing subpopulations colonizing or repopulating new breeding sites. For example, of the 45 tags recovered or observed on the Kuril Islands in 1967 (shortly after it had been re-populated); 40.0% originated from Tyuleniy Island, 26.7% from the Commander Islands, 20.0% from the Kuril Islands, and 13.3% percent from the Pribilof Islands (NPFSC 1975). Similarly, for tagged females observed breeding on San Miguel Island, 65.7% originated from the Pribilof Islands, 20.0% from the Commander Islands, and 14.3% from Tyuleniy Island (Table A-8 in Kozloff 1982). From a conservation biology perspective, the behavioural plasticity and high dispersal rates are important factors in determining the resilience of the northern fur seal populations (Pinsky et al. 2010).

The fur seal PVA incorporated information on the migration patterns of each subpopulation to assess their contribution to abundance off WCNA and Canadian waters. The analyses indicated there were sufficient numbers of animals (25% of total) from other subpopulations to sustain viable numbers even if the Pribilof Islands were to diminish to insignificant levels. Thus, the viability of northern fur seal population does not hinge on any one subpopulation. Indeed, there is a precedent for northern fur seals surviving without the Pribilof Island subpopulation. As Gentry (1998) noted, the islands used for breeding sites have undoubtedly changed during the

northern fur seal's 5-million year history.  The Pribilof Islands are only 2.2 million years old (Cox et al. 1966 cited in Gentry 1998), and they have been inundated at least four times by interglacial sea-level rises (Hopkins 1973 cited in Gentry 1998), and left standing as ice-covered mountains at sea twice by sea-level declines (Hopkins and Einarsson 1966 cited in Gentry 1998).

Another pinniped that has declined and been listed as endangered is the western population of Steller sea lions, but there are some important differences.  First, the northern fur seal population, which currently numbers about 1.2 million animals (Olesiuk 2007), is more than an order of magnitude larger than the western Steller sea lion population, which currently numbers about 50,000 animals (NMFS 2008).  Second, the declines of western Steller sea lions since the 1950s have been more widespread, greater in magnitude, and occurred rapidly.  At its peak, all 34 sea lion rookeries were declining, at an average rate of 17% per year over a 5-year period, resulting in an abrupt 60% drop in numbers (Goodman 2006; NMFS 2008).  In contrast, the declines in northern fur seals have been limited to one (albeit the largest) breeding site, and they have not been as steep or abrupt.  Over the last 60 years, the rate of decline of the Pribilof Island subpopulation has averaged less than 3% per year, and was steepest at about 5% per year during the 1950s due to an experimental kill of reproductive females.  Finally, the western Steller sea lion population has exhibited very little scope for recovery, with only modest increases of about 3% observed in recent years (NMFS 2008).  In contrast, northern fur seals have undergone two major depletions, both due to over-harvesting of females, but subsequently recovered at a rate of about 8% when the female harvests were terminated (Gentry 1998).

Although the northern fur seal is not at risk of extinction or extirpation from its Canadian range, the continued decline of the once dominant herd on the Pribilof Islands nevertheless represents a serious conservation concern.  Pup production on the Pribilof Islands is currently at less than 20% of historic peak levels, and pup counts continue to decline on St. Paul Island.  However, endangered species legislation like SARA or ESA do not contain provisions for maintaining species at peak or even high population levels, are thus not the appropriate mechanism for protecting abundant, widely distributed species like the northern fur seal.  There is more appropriate legislation that provides broader protection to and conservation of marine resources and ecosystems.  For example, the Marine Mammal Protection Act (MMPA) in the U.S. stipulates that marine mammal populations be maintained at maximum net productivity levels.  Northern fur seals on Pribilof Islands has been designated as depleted under MMPA, and identified as a strategic stock for management and research.  Similar provisions have been used in Canada. For example, Hammill and Stenson (2002) developed a precautionary framework and proposed reference points for managing Atlantic seals, and such an approach needs to be adopted for managing marine mammal populations in Canada that are not at risk of extinction but there are conservation concerns.

## ACKNOWLEDGEMENTS

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*Table 1.* *Tag deployment data for the 1958 to 1968 cohorts of northern fur seals (from NPFSC 1962, 1969, 1971, 1975; Lander 1980).*

| Cohort | Pribilof (St. Paul) Island | | | | Pribilof (St. George) Island | | | | Commander (Medny) Island | | | | Commander (Bering) Island | | | | Tuyleny (Tyuleniy) Island | | | | Kuril Island | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Born | Tagged | Rate | | Born | Tagged | Rate | | Born | Tagged | Rate | | Born | Tagged | Rate | | Born | Tagged | Rate | | Born | Tagged | Rate |
| 1958 | 387,000 | 44,923 | 11.6% | | 84,189 | 9,994 | 11.9% | | 14,187 | 2441 | 17.2% | | 9,710 | 2,446 | 25.2% | | 32,106 | 7225 | 22.5% | | | | |
| 1959 | 335,000 | 39,901 | 11.9% | | 72,877 | 9,980 | 13.7% | | 17,880 | 3,278 | 18.3% | | 18,800 | 4,693 | 25.0% | | 35,122 | 9015 | 25.7% | | | | |
| 1960 | 320,000 | 47,989 | 15.0% | | 69,614 | 11,992 | 17.2% | | 19,457 | 7,609 | 39.1% | | 15,688 | 3,272 | 20.9% | | 37,944 | 10376 | 27.3% | | | | |
| 1961 | 342,335 | 39,933 | 11.7% | | 74,473 | 9,988 | 13.4% | | 23,462 | 7,120 | 30.3% | | 14,400 | 3,949 | 27.4% | | 39,987 | 10472 | 26.2% | | 1,540 | 0 | 0.0% |
| 1962 | 300,828 | 39,928 | 13.3% | | 65,443 | 9,980 | 15.2% | | 25,500 | 7,720 | 30.3% | | 26,000 | 7,820 | 30.1% | | 43,879 | 10756 | 24.5% | | 2,618 | 0 | 0.0% |
| 1963 | 262,498 | 19,978 | 7.6% | | 57,105 | 4,993 | 8.7% | | 27,303 | 3,999 | 14.6% | | 27,586 | 5,639 | 20.4% | | 50,105 | 11295 | 22.5% | | 3,388 | 0 | 0.0% |
| 1964 | 283,922 | 19,998 | 7.0% | | 61,765 | 4,993 | 8.1% | | 29,233 | 6,522 | 22.3% | | 29,269 | 6,531 | 22.3% | | 50,786 | 10890 | 21.4% | | 4,466 | 0 | 0.0% |
| 1965 | 253,768 | 10,000 | 3.9% | | 55,205 | - | 0.0% | | 31,710 | 4,488 | 14.2% | | 26,840 | 3,798 | 14.2% | | 48,938 | 8005 | 16.4% | | 2,618 | 0 | 0.0% |
| 1966 | 319,045 | 10,000 | 3.1% | | 69,406 | 2,499 | 3.6% | | 30,684 | 7,928 | 25.8% | | 30,345 | 7,840 | 25.8% | | 44,949 | 12193 | 27.1% | | 3,388 | 1500 | 44.3% |
| 1967 | 291,000 | 9,980 | 3.4% | | 63,305 | 2,492 | 3.9% | | 23,374 | 7,673 | 32.8% | | 31,156 | 7,972 | 25.6% | | 56,040 | 17585 | 31.4% | | 3,388 | 1588 | 46.9% |
| 1968 | 235,000 | 9,200 | 3.9% | | 51,123 | 2,475 | 4.8% | | 26,540 | 8,494 | 32.0% | | 34,319 | 6,994 | 20.4% | | 46,019 | 9400 | 20.4% | | 21,406 | 3,088 | 14.4% |
| Total | 3,330,396 | 291,830 | 8.8% | | 724,504 | 69,386 | 9.6% | | 269,330 | 67,272 | 25.0% | | 264,113 | 60,954 | 23.1% | | 485,875 | 117,212 | 24.1% | | 1,540 | 0 | 0.0% |

**Table 2.** Tag recoveries from the 1958 to 1968 cohorts during the NPFSC pelagic research collections during 1958-1974 (unpublished data), and tag resightings on reproductive females at San Miguel Island during 1968-1982 (from Appendix Table A-8 in Kozoff 1982).

| Cohort | Pribilof (St. Paul) Island | | | Pribilof (St. George) Island | | | Commander (Medny) Island | | | Commander (Bering) Island | | | Tuyleny (Tyuleniy) Island | | | Kuril Island | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | WCNA | San Miguel | Japan | WCNA | San Miguel | Japan | WCNA | San Miguel | Japan | WCNA | San Miguel | Japan | WCNA | San Miguel | Japan | WCNA | San Miguel | Japan |
| 1958 | 22 | 0 | 14 | 9 | 0 | 3 | 0 | 0 | 11 | 0 | 0 | 11 | 0 | 0 | 131 | 0 | 0 | 0 |
| 1959 | 18 | 0 | 7 | 4 | 0 | 3 | 0 | 0 | 13 | 0 | 0 | 13 | 0 | 0 | 91 | 0 | 0 | 0 |
| 1960 | 15 | 1 | 14 | 4 | 0 | 1 | 0 | 0 | 19 | 0 | 1 | 15 | 0 | 0 | 138 | 0 | 0 | 0 |
| 1961 | 34 | 7 | 12 | 11 | 1 | 2 | 0 | 0 | 31 | 0 | 0 | 21 | 0 | 0 | 150 | 0 | 0 | 0 |
| 1962 | 16 | 2 | 8 | 9 | 0 | 1 | 0 | 0 | 30 | 1 | 0 | 11 | 0 | 0 | 53 | 0 | 0 | 0 |
| 1963 | 7 | 0 | 2 | 2 | 0 | 1 | 1 | 0 | 12 | 0 | 0 | 11 | 0 | 0 | 73 | 0 | 0 | 6 |
| 1964 | 11 | 1 | 4 | 2 | 0 | 1 | 1 | 0 | 11 | 3 | 0 | 18 | 0 | 0 | 39 | 0 | 0 | 2 |
| 1965 | 8 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 5 | 2 | 0 | | 1 | 1 | 38 | 0 | 0 | 0 |
| 1966 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 0 | 5 | 1 | 0 | 10 | 0 | 1 | 28 | 0 | 0 | 1 |
| 1967 | 10 | 3 | 0 | 2 | 1 | 0 | 0 | | 6 | 1 | 0 | 11 | 0 | 0 | 22 | 0 | 0 | 1 |
| 1968 | 8 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 2 | 0 | 0 | 9 | 0 | 0 | 4 | 0 | 0 | 0 |
| Total | 149 | 17 | 61 | 46 | 4 | 12 | 4 | 2 | 145 | 8 | 1 | 130 | 1 | 2 | 767 | 0 | 0 | 10 |

**Table 3.** *Tags recovered off WCNA (including San Miguel Island), calculation of proportion of animals originating from each breeding site adjusted for tagging rates, and propensity of animals to migrate along WCNA adjusted for differences in size of sites (see text for details).*

| Site | Tags Recovered | | Tagging Rate | Proportion of Animals | Pups Born | Migration Propensity |
|---|---|---|---|---|---|---|
| | Number | % | | | | |
| Pribilof Islands | 216 | 92.3% | 8.9% | 97.0% | 368,627 | 1.000 |
| Bogoslof Island | - | - | - | 0.0% | 0 | - |
| Commander Islands | 15 | 6.4% | 24.0% | 2.5% | 48,495 | 0.198 |
| Kuril Islands | 0 | 0.0% | 14.4% | 0.0% | 3,058 | 0.000 |
| Tuyleny (Robben) Island | 3 | 1.3% | 24.1% | 0.5% | 44,170 | 0.043 |
| Total | 234 | 100.0 | | 100.0% | 464,350 | |

**Table 4.** *Estimated proportion of animals migrating along WCNA originating from each breeding subpopulation during the NPFSC pelagic research collections in 1958-74 (top) and based on the most recent pup counts in 2005-2011 (bottom).*

| Site | NPFSC Pelagic Sampling 1958-74 | | |
|---|---|---|---|
| | Pup Production | Migration Propensity | Relative Abundance |
| Pribilof Islands | 368,447 | 1.000 | 97.5% |
| Bogoslof Island | 0 | 1.000 | 0.0% |
| Commander Islands | 48,495 | 0.198 | 2.3% |
| Kuril Islands | 3,058 | 0.043 | 0.0% |
| Tyuleniy Island | 44,170 | 0.043 | 0.2% |
| Total | 464,170 | | |
| | | | |
| | **Most Recent Counts 2005-2011** | | |
| Pribilof Islands | 111,600 | 1.000 | 75.0% |
| Bogoslof Island | 22,905 | 1.000 | 15.4% |
| Commander Islands | 59,805 | 0.198 | 8.0% |
| Kuril Islands | 27,090 | 0.043 | 0.8% |
| Tyuleniy Island | 30,000 | 0.043 | 0.9% |
| Total | 251,495 | | 100.0% |

*Table 5.*  *Calculation of the number of northern fur seals wintering off WCNA and migrating through Canadian waters based most recent surveys in 2005-2011 (see text for details).*

| Parameter | Estimate | Soruce |
|---|---|---|
| Pribilof Island Pup Production | 111,600 | Towell et al. (2010) |
| Non-Pup:Pup Multiplier | 4.47 | Loughlin et al. (1996) |
| Pribilof Island Total Population Size | 499,000 | Calculated from above 2 rows |
| Proportion of Pribilof Population wintering off WCNA | 52% | Olesiuk (2008, this study) following methods in Antonelis and Perez (1994) |
| Number of Pribilof animals wintering off WCNA | 259,000 | Calculated from above 2 rows |
| Proportion of animals wintering off WCNA from Pribilof Islands | 75% | From Table 3 |
| Total abundance off WCNA | 346,000 | Calculated from above 2 rows |
| Proportion of WCNA seals migrating through Canadian waters at peak in May | 34% | Olesiuk (2008) based on NPFSC sighting surveys |
| Peak seasonal abundance in Canada | 118,000 | Calculated from above 2 rows |

**Table 6.** *Summary of Population Viability Analyses for each subpopulation, indicating length of the time-series of pup counts (years), estimated intrinsic rate of increase, whether there was density dependence, total mean square error (MSE), estimated measurement error (ME), estimated risk of quasi-extinction within 100 and 120 years, and estimated mean time to extinction (years). For the Pribilof Islands, the upper numbers are for St. Paul Island and the lower numbers for St. George Island.*

| Site | Time Series (yrs) | N | Rate | Density Effects | MSE | ME | Risk 100 Years | Risk 120 Years | Mean Time |
|---|---|---|---|---|---|---|---|---|---|
| Pribilof | 10 | 5<br>5 | -0.010<br>-0.012 | N<br>N | 0.00065<br>0.00274 | 0.00027<br>0.00217 | 0.29% | 2.07% | 199 |
| Pribilof | 30 | 20<br>15 | -0.021<br>-0.027 | N<br>N | 0.01045<br>0.00636 | 0.00660<br>0.00397 | 0.13% | 1.68% | 152 |
| Pribilof | 50 | 40<br>19 | <br>-0.027 | N | 0.01244<br>0.00721 | 0.00735<br>0.00366 | 0.10% | 1.17% | 161 |
| Bogoslof | 30 | 9 | 0.464-0.152 | Y | 0.17301 | 0.00000 | 0.00% | 0.00% | - |
| Commander | 10 | 6 | 0.017 | N | 0.01742 | 0.00000 | 0.42% | 0.84% | 486 |
| Commander | 30 | 17 | -0.003 | N | 0.00699 | 0.00000 | 0.00% | 0.03% | 583 |
| Commander | 50 | 37 | 0.011 | N | 0.00749 | 0.00000 | 0.00% | 0.00% | 521 |
| Tyuleniy | 10 | 9 | 0.055 | N | 0.00000 | 0.00000 | 0.00% | 0.00% | - |
| Tyuleniy | 30 | 28 | 0.029 | N | 0.00345 | 0.00000 | 0.00% | 0.00% | - |
| Tyuleniy | 50 | 47 | 0.014 | N | 0.01472 | 0.00000 | 0.03% | 0.05% | 478 |
| Kuril | 30 | 14 | 0.013 | N | 0.02529 | 0.02052 | 0.00% | 0.00% | 000's |
| Kuril | 50 | 28 | 0.032 | N | 0.06456 | 0.02052 | 0.35% | 0.52% | 000's |
| Canada | 10 | - | - | - | - | - | 0.00% | 0.00% | - |
| Canada | 30 | - | - | - | - | - | 0.00% | 0.00% | - |
| Canada | 50 | - | - | - | - | - | 0.00% | 0.00% | - |
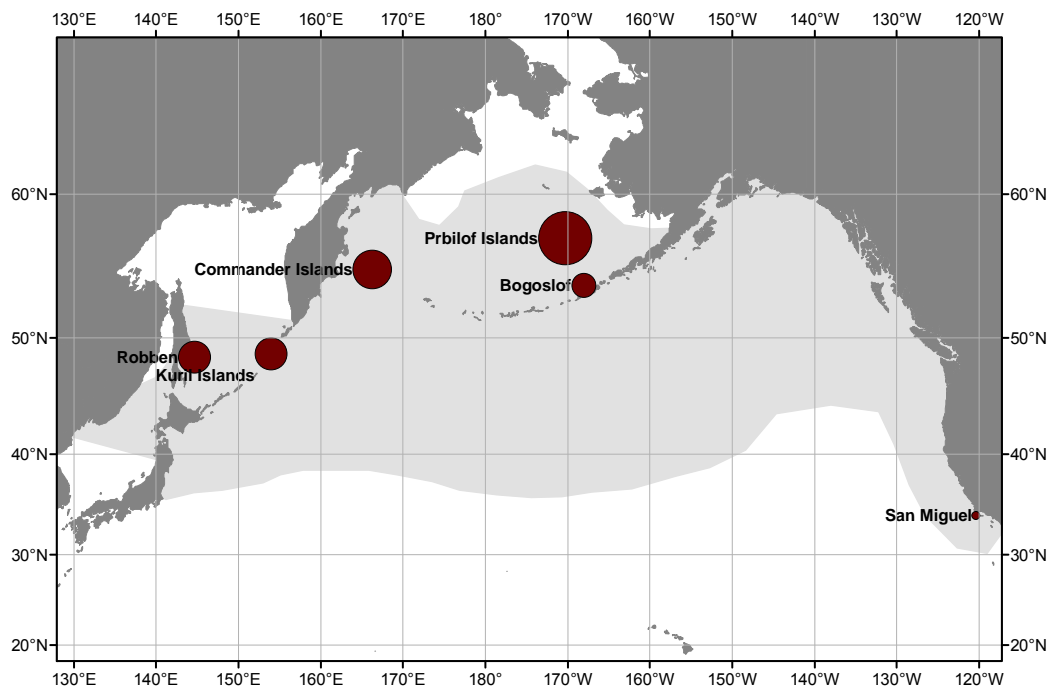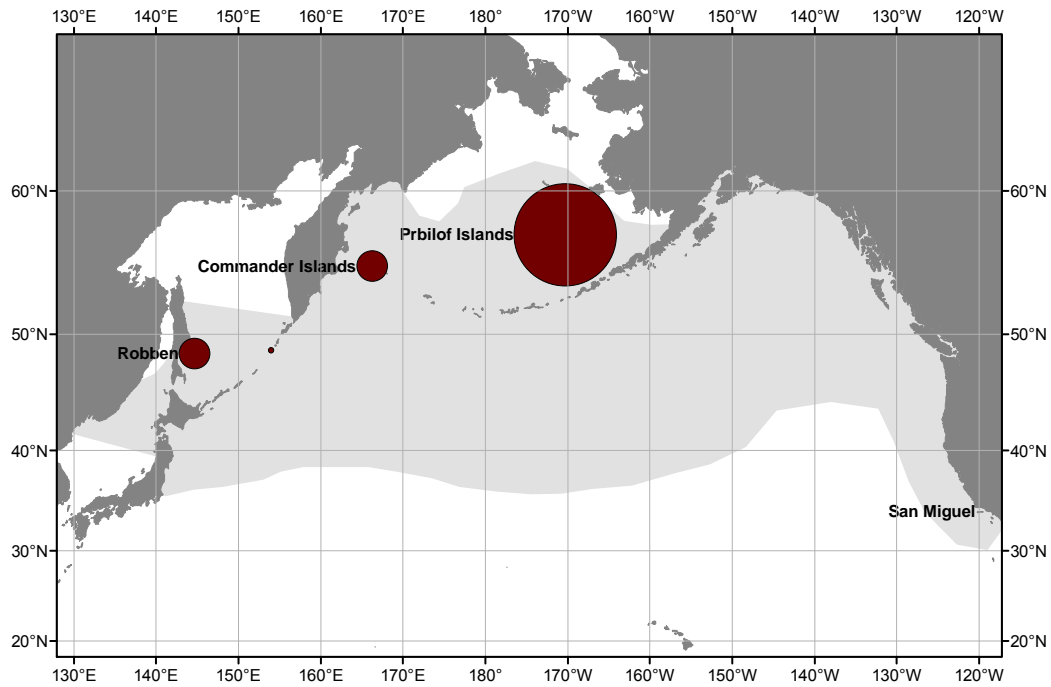
**Figure 1**. *Map showing the distribution of major breeding sites in 1960 and in 2010. Red circles are drawn proportional to pup production. Grey area shows approximate pelagic distribution.*
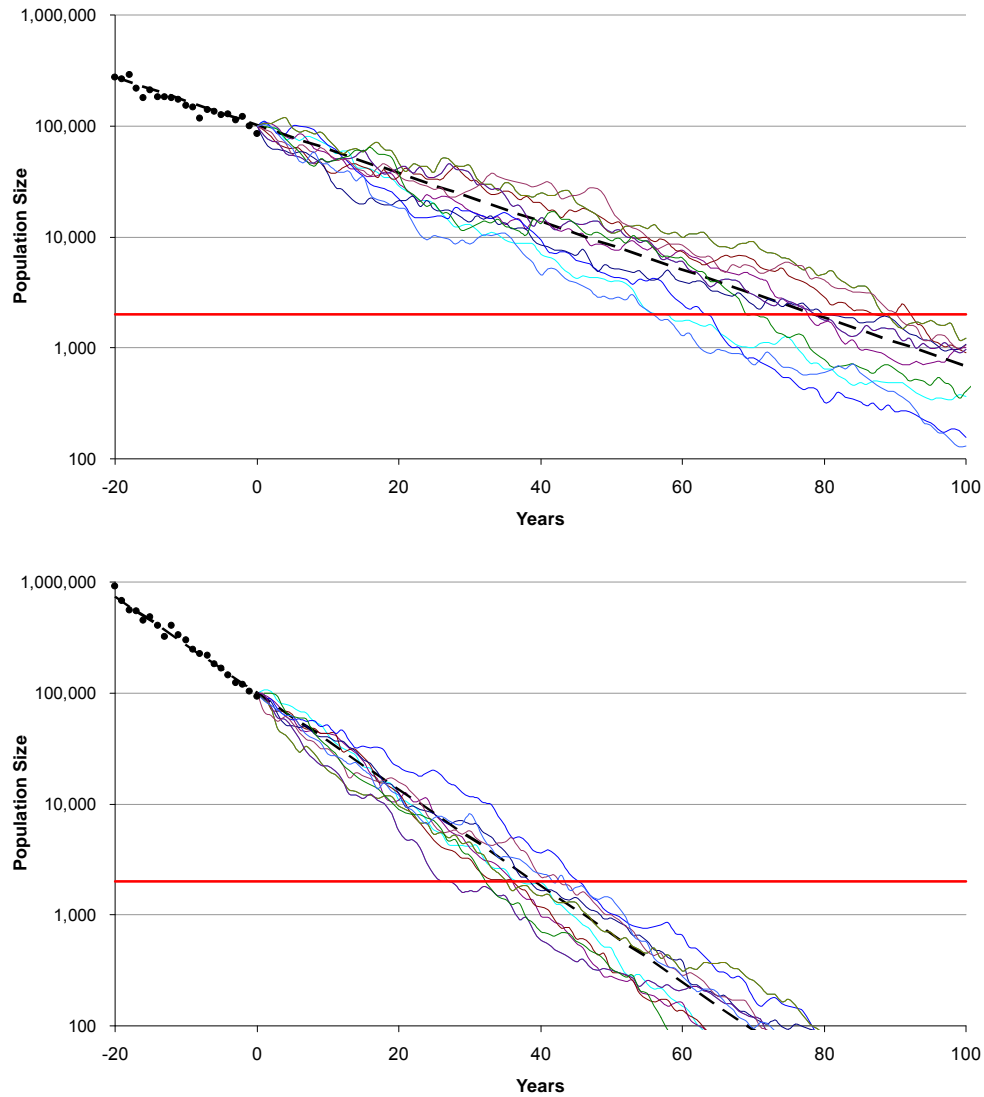
**Figure 2.** *Hypothetical example for the diffusion model showing the effects of population size ($N_0$), trend (r) and variability ($\sigma^2$) in determining risk of quasi-extinction. The black circles denote survey counts fitted to a 20-year time-series prior to time 0, the black dashed black line represents the trajectory, and the coloured lines represent 10 random realizations showing drift. The red horizontal line denotes the threshold for quasi-extinction, for this example set to 2,000 animals. The first panel is the base case ($N_0$=100,000, r=-0.05 and $\sigma^2$=0.1). The remaining panels illustrate how risk of quasi-extinction can be increased by decreasing r to -0.10 (second panel), decreasing $N_0$ to 5,000 (third panel) or increasing $\sigma^2$ to 0.2.*
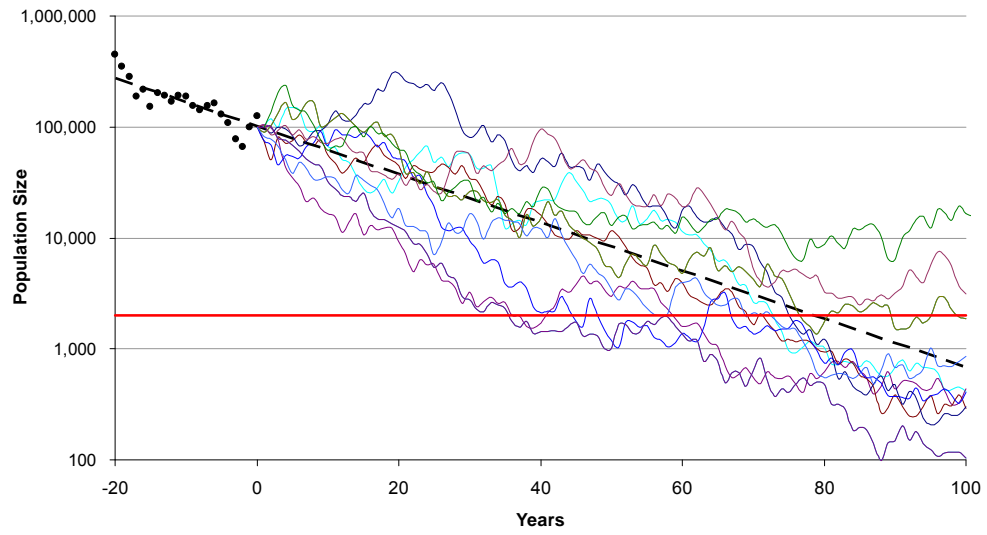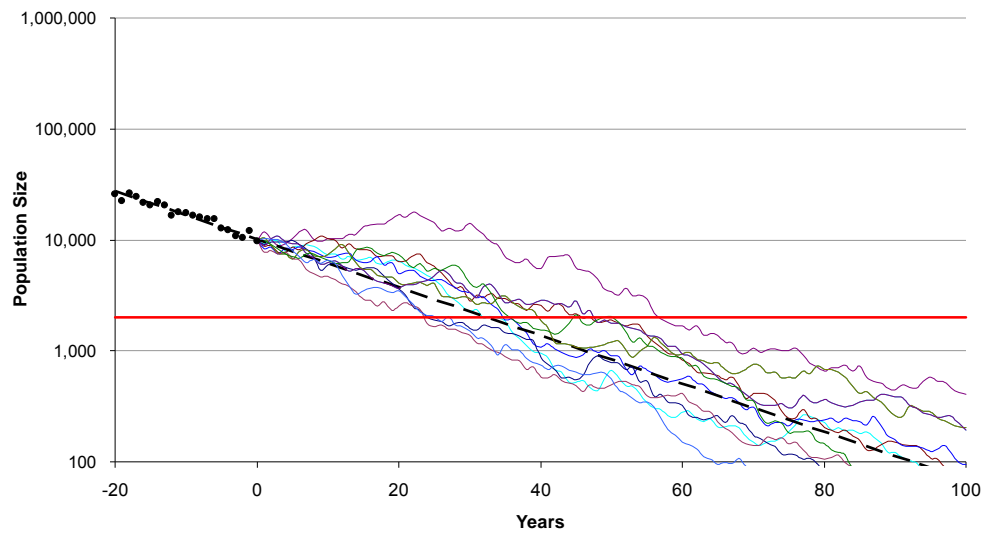
**Figure 2.** *Continued.*
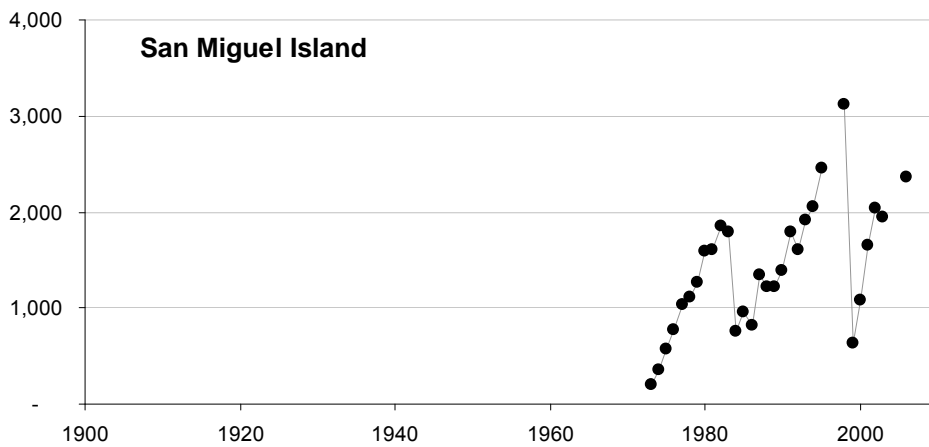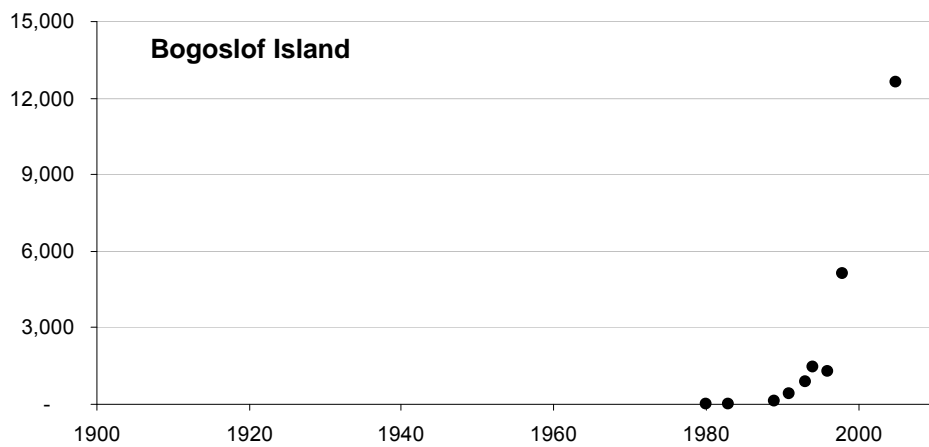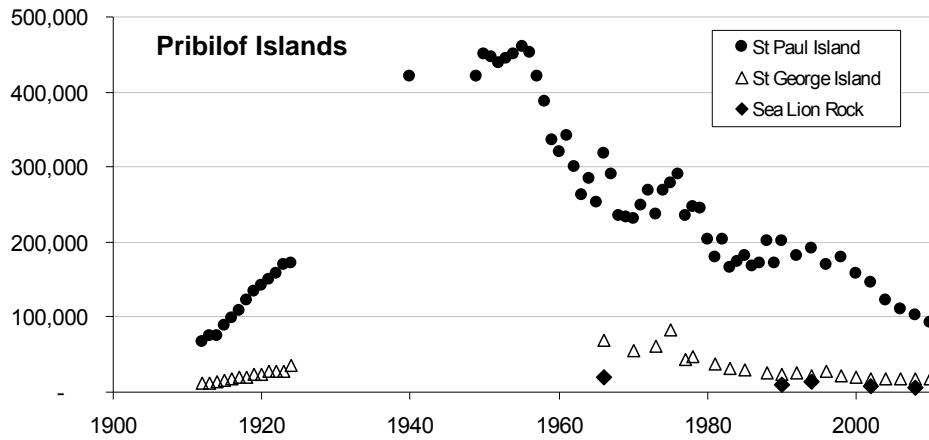
*Figure 3*.  Northern fur seal pup counts for each breeding site (from Lander 1980a; Kozloff 1982, 1985, 1986; Kozloff and Kajimura 1986; Kajimura 1990a, 1990b; Kajimura and Sinclair 1992; Sinclair 1993, 1994a, 1994b, 1996, 1997a, 1997b; Sinclair and Robson 1999; Robson 2000, 2001, 2002; Testa 2005, 2007, 2008; Burkanov and Calkins 2007; Burkanov et al. 2007; Kuzin 2010; and R. Ream and T. Gelatt, National Marine Mammal Laboratory, Seattle, pers. comm).  Counts dating back to the early 1900's are shown to provide context, but only counts made within the last 50 years were used in the PVA.
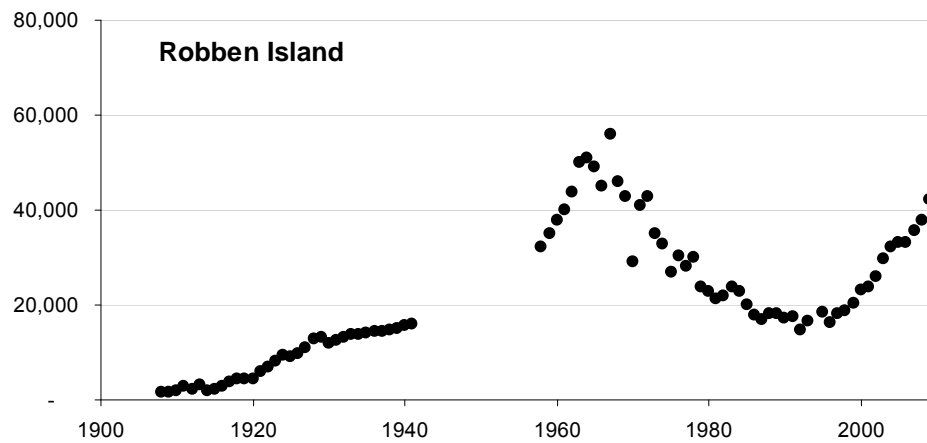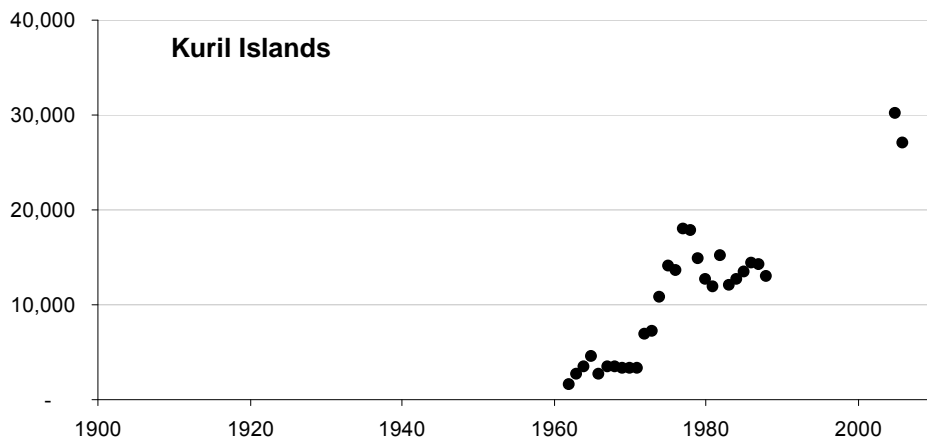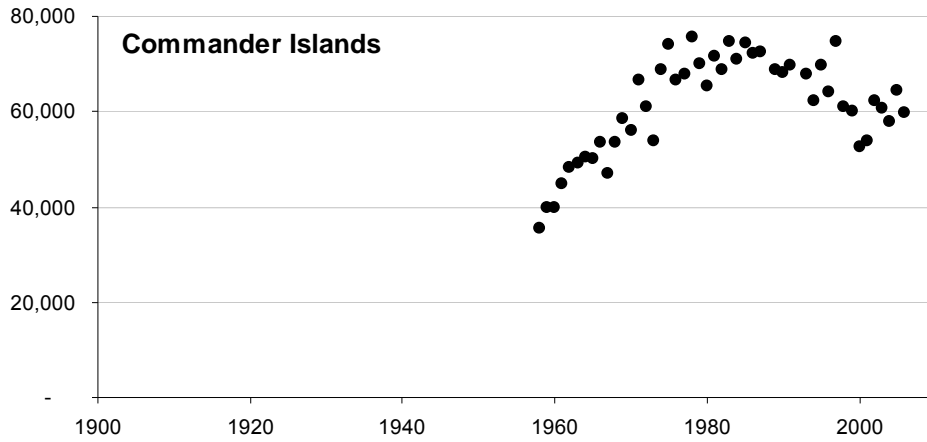
**Figure 3**. *Continued.*
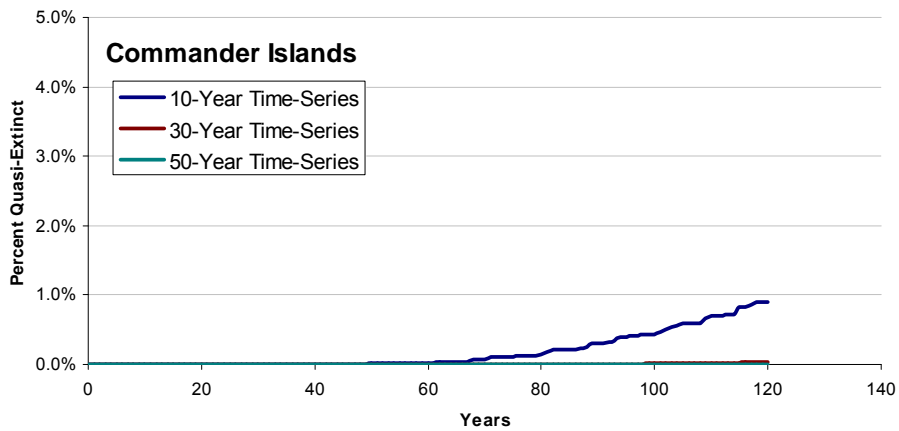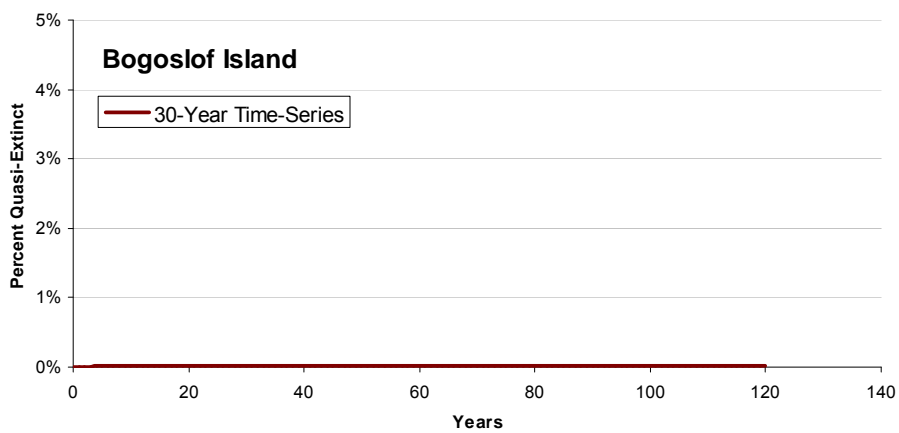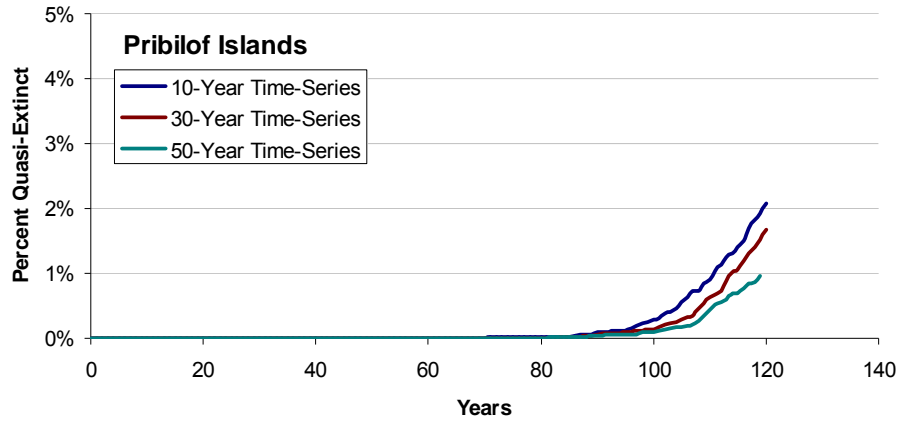
**Figure 4**. *Plots showing the cumulative probability of quasi-extinction within the next 100 and 120 years for each subpopulation, and for seals migrating through Canadian waters.*
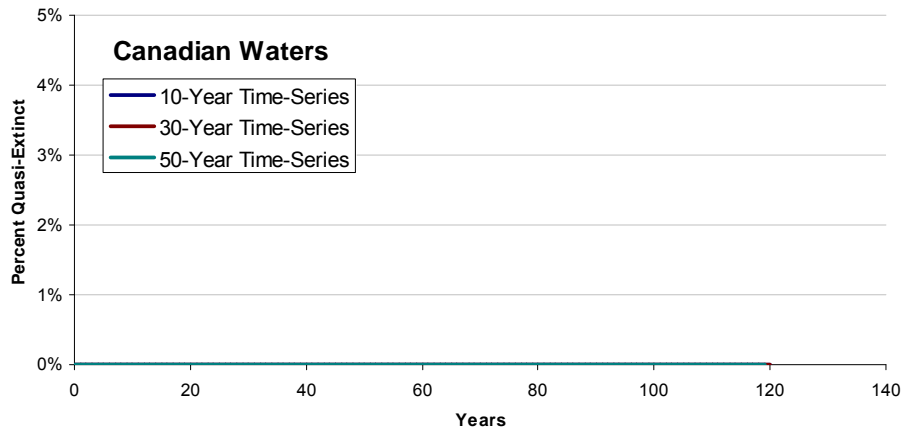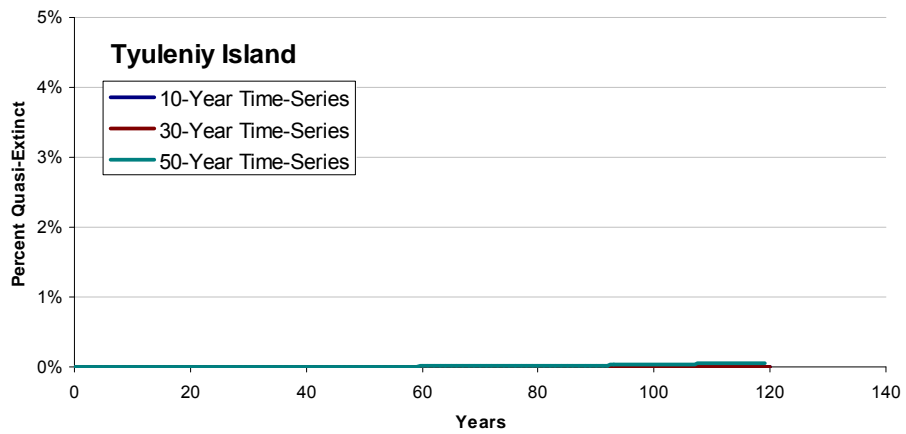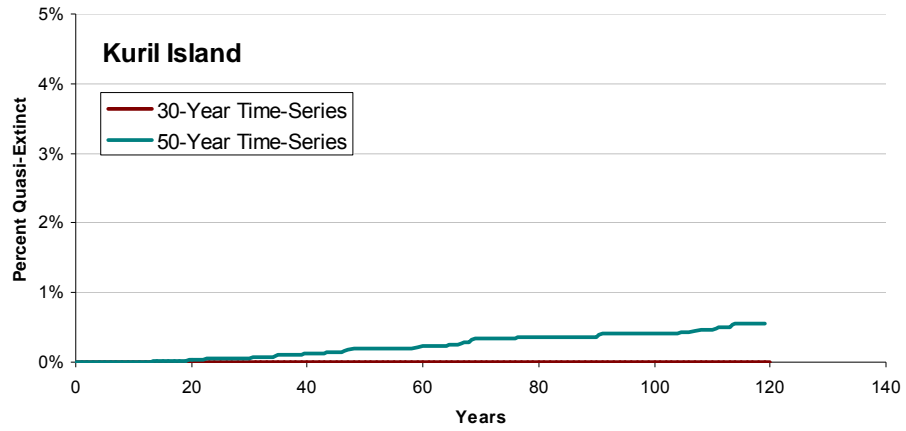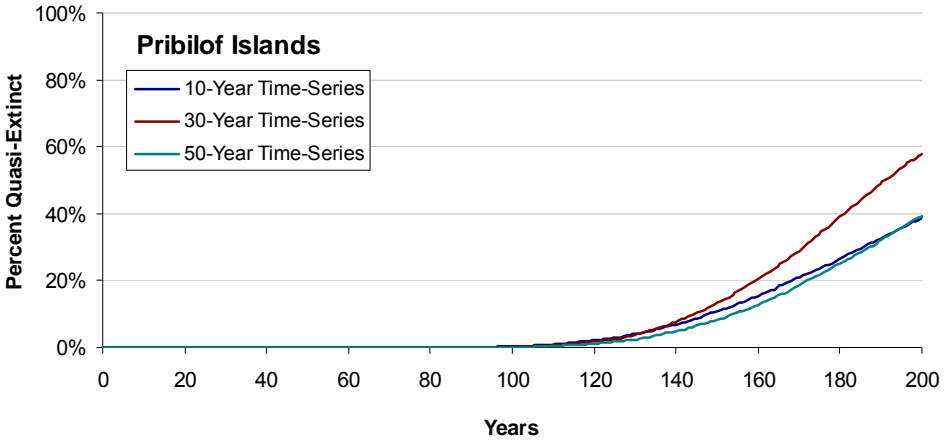
***Figure 4***. *Continued.*

**Figure 5**.  *Plot showing the escalating cumulative probability of quasi-extinction of the Pribilof Island subpopulation within the next 200 years if the recent rate of declines were to persist into the next century.*