Comparative Demography and Viability of Northeastern Pacific Resident Killer Whale Populations at Risk

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COMPARATIVE DEMOGRAPHY AND VIABILITY OF NORTHEASTERN PACIFIC RESIDENT KILLER WHALE POPULATIONS AT RISK

by

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ABSTRACT

Vélez-Espino, L.A., Ford, J.K.B., Araujo, H.A., Ellis, G., Parken, C.K., and Balcomb, K.C. 2014. Comparative demography and viability of northeastern Pacific resident killer whale populations at risk. Can. Tech. Rep. Fish. Aquat. Sci. 3084: v + 58 p.

Two distinct populations of resident killer whales (*Orcinus orca*) in the northeastern Pacific Ocean have been identified in Canada and the U.S. as being of conservation concern. In this paper we quantify the differences in demographic rates between southern residents (SRKW) and northern residents (NRKW) and merge perturbation and population viability analyses to study population responses to potential management actions targeting specific vital rates. The life cycles of these two populations were modeled as two-sex stage-structured models based on high-quality demographic data encompassing one killer whale generation (25 years; 1987-2011). Projection matrices were used to compute stochastic population growth and run stochastic simulations of extinction risk and recovery probabilities. Expected population growth rates are 0.91% annual decline ($\lambda = 0.9909$; 95% CI: 0.9719-1.0081) for SRKW and 1.58% annual increase ($\lambda = 1.0158$; 95% CI: 1.0027-1.0285) for NRKW. Conservatively, and under status-quo conditions, SRKW's population size is expected to reach 75 individuals in a generation, with an extinction risk of 49% and an expected minimum abundance of 15 during a 100-year period, whereas NRKW's population size could reach 400 individuals in a generation in the absence of density dependence, with an extinction risk of zero and an expected minimum abundance of 238 individuals during a 100-year period. SRKW's lower realized and expected population growth as well as its lower viability relative to NRKW was mainly ascribed to SRKW's lower production and survival of viable calves, lower proportion of juveniles transitioning into young reproductive females, and greater vital rate variances.

RÉSUMÉ

Vélez-Espino, L.A., Ford, J.K.B., Araujo, H.A., Ellis, G., Parken, C.K., et Balcomb, K.C. 2014. Comparative demography and viability of northeastern Pacific resident killer whale populations at risk. Can. Tech. Rep. Fish. Aquat. Sci. 3084: v + 58 p.

Deux populations distinctes d'épaulards résidents (*Orcinus orca*) dans le nord-est de l'océan Pacifique ont été désignées au Canada et aux États-Unis comme étant préoccupantes sur le plan de la conservation. Dans le présent document, nous quantifions les différences dans les taux démographiques entre les populations résidentes du sud et les populations résidentes du nord, et nous combinons des analyses de la perturbation et de la viabilité des populations pour étudier les réponses des populations aux mesures de gestion potentielles visant des indices vitaux précis. Les cycles biologiques de ces deux populations ont été modélisés en utilisant des structures par stades selon le sexe basées sur des données démographiques de haute qualité englobant une génération d'épaulards (25 ans; 1987-2011). Des matrices de projection ont été utilisées pour compiler la croissance stochastique des populations et exécuter des simulations stochastiques du risque d'extinction et des probabilités de rétablissement. Les taux de croissance de la population prévus sont un déclin annuel de 0,91 % (λ = 0,9909; intervalle de confiance [IC] de 95 % : 0,9719-1,0081) pour la population d'épaulards résidents du sud et une augmentation annuelle de 1,58 % (λ = 1,0158; IC de 95 % : 1,0027-1,0285) pour la population d'épaulards résidents du nord. De manière prudente, et dans un contexte de conditions inchangées, la taille de la population d'épaulards résidents du sud devrait atteindre 75 individus en une génération, avec un risque d'extinction de 49 % et une abondance minimale prévue de 15 individus sur une période de 100 ans, tandis que la taille de la population d'épaulards résidents du nord devrait atteindre 400 individus en une génération en l'absence de dépendance à la densité, avec un risque d'extinction de zéro et une abondance minimale prévue de 238 individus sur une période de 100 ans. La croissance de la population plus faible prévue et réelle de la population d'épaulards résidents du sud de même que sa viabilité plus basse par rapport à la population d'épaulards résidents du nord sont principalement attribuables à la survie et à la production moindres de veaux viables, à la plus faible proportion de juvéniles devenant de jeunes femelles reproductrices et à la plus grande variance de l'indice vital.

1.0. INTRODUCTION

Two distinct populations of resident killer whales (*Orcinus orca*) in the northeastern Pacific Ocean have been identified in Canada and the U.S. as being of conservation concern. The Southern Resident Killer Whale (SRKW) population is currently listed as endangered under the U.S. Endangered Species Act on the grounds of its small population size and vulnerability to demographic stochasticity and catastrophic events such as oil spills (NMFS 2008). In Canada, under the Species At Risk Act (COSEWIC 2008), SRKW is listed as endangered due to its small and declining population size while the Northern Resident Killer Whale (NRKW) population is listed as threatened due to its small population size. The major threats identified for these two populations are nutritional stress associated with prey abundance levels and availability, particularly Chinook salmon (*Oncorhynchus tshawytscha*) (COSEWIC 2008, Ford et al. 2010a, 2010b), pollution and contaminants, and disturbances from vessels and sound (COSEWIC 2008, NMFS 2008).

SRKW have been identified from Monterey Bay, California to Langara Island, British Columbia to Southeast Alaska, an overall range of approximately 2000 km along the coast, whereas the range of NRKW includes coastal waters from Glacier Bay, Alaska, to Gray's Harbor, Washington State, a linear distance of approximately 1500 km along the west coast (Figure 1; Ford 2006). An important difference in the population-size trajectories of these two populations is that, in spite of their home range overlap and potential access to similar resources, SRKW has remained at a population size of less than 100 individuals for the last four decades with an average of 85 individuals in the last decade. NRKW population size has been generally increasing for the last four decades with 268 individuals at the end of 2011 (Figure 1). The U.S. recovery plan for SRKW required an average population growth rate of 2.3 percent per year for 14 years for downlisting and 28 years for delisting (NMFS 2008). In Canada, specific viability criteria are not provided in the recovery strategy, where the recovery objectives for these two killer whale populations (RKW; hereafter used to refer to both SRKW and NRKW) are to ensure their long-term viability (DFO 2008).

Demographic data for RKW have been compiled in long-term registries maintained by the Cetacean Research Program, Pacific Biological Station, Fisheries and Oceans Canada (for NRKW), and the Center for Whale Research, Friday Harbor, WA (for SRKW). These registries are based on annual population surveys using photo-identification of individuals. Surveys have occurred annually without interruption since 1973 for NRKW and 1974 for SRKW. Each year, all observed animals are assessed for their status (e.g., reproductive state) and to document new births and deaths. Since these field studies began, 740 whales have been documented, 356 of which were alive in 2011. Of these, about 85% were born since the study began. These remarkable demographic data, unique because of their temporal extent and accounting of all individuals in these populations, have enabled important ecological studies (e.g., Bigg et al. 1990, Ford et al. 2005, 2010b) and the development of RKW population models (Brault & Caswell 1993, Krahn et al. 2002, 2004, Olesiuk et al. 1990, 2005).

Our goal is to identify the current population status of RKW. To accomplish this, we build on previous population studies through the implementation of a novel approach that merges perturbation analyses with population viability analysis (PVA), incorporates demographic and environmental stochasticity, and uses up-to-date RKW data. This undertaking is envisioned to contribute to our understanding of RKW population dynamics and to inform future conservation and management decisions. Our specific objectives are (i) to quantify the differences in demographic rates between SRKW and NRKW that could explain SRKW's small population size and limited population growth; (ii) to determine the relative influence of RKW's vital rates on expected population growth; and, (iii) to conduct assessments of extinction risk and probability of recovery while exploring population responses to demographic perturbations.

Our study of RKW demography is based on matrix population models. Future population dynamics, including probability of recovery and extinction risk, ideally require demographic models because these are the only framework that can integrate the vital rates that determine expected change in population size (Caswell 2001). Matrix models constitute a demographic approach to the quantitative analysis of population responses to perturbations that has proven to be robust to many parameter uncertainties (de Kroon et al. 2000, Heppell 2007) and valuable and efficient tools to address relevant management questions related to conservation and recovery of aquatic populations (Getz & Haight 1989, Vélez-Espino & Koops 2009b), mammals in general (Heppell et al. 2000, Oli & Dobson 2003) and cetaceans in particular (e.g., Brault & Caswell 1993, Caswell et al. 1998, Fujiwara & Caswell 2001). Our approach entails four steps. First, employ individual-based data to generate vital-rate probability distributions. Second, use these vital rate distributions to build stochastic matrix models representing separately the dynamics of SRKW and NRKW. Third, use stochastic projection matrices to compute expected population growth rates and to explore future population dynamics using population viability analysis (PVA). Lastly, evaluate the response of population growth and viability to perturbations on relevant vital rates.

2.0. METHODS

2.1. Selected time period for demographic analyses

Demographic analyses focused on data from 1987 to 2011, which represented a RKW generation (using life-table methods, we estimated a generation time of ~25 years for both SRKW and NRKW) and included high quality data with ~75% of the RKW individuals alive in 2011 born during the selected time period. This step was important because it allowed us to include mostly census data generated by direct observations and to remove from the analyses the effect on stage structures caused by the large live-capture RKW fisheries in the 1960's and 1970's. Demographic data for the earlier years of RKW studies were thoroughly reconstructed to fill age information gaps (see Olesiuk et al. 1990). The reconstruction procedures used in the past relied on numerous assumptions such as (i) female age at first birth remained constant, (ii) genealogical trees by Bigg et al. (1990) were accurate, (iii) calving intervals remained constant, and (iv) survival rates remained constant. For count-based realized population growth (*r*) some of these assumptions may have a small weight but they matter for demographic modelling. In addition, RKW population surveys begun right after the end of the killer whale live-capture fishery, which for resident killer whales lasted from 1962 to 1973 (Bigg 1975, Olesiuk et al. 1990). This fishery was heavily biased towards juveniles and young males and impacted more heavily the SRKW, thus affecting not only population size but also the structure of the population. This is crucial for population projections since the population structure observed in the first years of the time series is radically different from that of the present (Appendix A). Presently, there is no live capture of resident killer whales and therefore the effects of this stressor on population structure and demographic rates are not a factor for future RKW population dynamics.

2.2. Killer whale matrix population modeling

Our analyses are based on stage-structured models because not all age classes are represented in any given year given the longevity and small size of these two populations, particularly that of SRKW. Greater contrast between demographic parameters is expected from a smaller number of discrete life stages in such a long-lived species that otherwise would require an age-structured projection matrix with a minimum of 50 age classes. In addition, design and implementation of potential management actions would benefit from these greater contrasts by focusing management actions on life stages rather than on individual age groups. The main assumption implicit in stage-structured models, is that all individuals within a stage are demographically comparable. It has been demonstrated that failure of this assumption is important for analyses of transient dynamics but much less for the analysis of asymptotic dynamics such as the estimation of expected population growth rates and perturbation analyses (Caswell 2001).

The life cycles of SRKW and NRKW were modeled separately because these two populations are demographically discrete with no interchange of individuals between them (Bigg et al. 1990). There is no evidence of NRKW males fathering SRKW offspring, or vice versa, therefore reinforcing the demographically isolated nature of these two populations (Ford et al. 2011). SRKW and NRKW populations are also acoustically, genetically, and culturally distinct (Barrett-Lennard & Ellis 2001, Ford et al. 1998, 2000, 2011). RKW populations dynamics were represented by two-sex stage-structured models with seven life stages: (1) calves (individuals in the first year of life); (2) juveniles (immature individuals ages 1-9; mostly undetermined sex); (3) young reproductive females (ages 10-30); (4) old reproductive females (ages 31-50); (5) post-reproductive females (51 year old and older); (6) young mature males (ages 10-21); and, (7) old mature males (22 year old and older). Age intervals are similar to those in Krahn et al. (2004), but we split the reproductive females stage into two stages (young and old) to account for differences in reproductive potential associated to reproductive senescence (Ward et al. 2010) and, based on current data, updated the age at maturity (10) and maximum reproductive age (50) of females. Similarly, mature males were split into two stages because there is evidence for a clear increase in male reproductive success with age (Ford et al. 2011).

The life cycle of RKW is shown in Figure 2 where P_i is the probability of surviving and remaining in stage *i*, G_i is the probability of surviving and moving to the next stage, and F_i is the fertility rate of stage i. A stage-structured model requires defining three lower-level parameters, namely vital rates: σ_i as the annual survival probability of an individual in stage *i*, γ_i as the probability of moving from stage *i* to stage *j* given σ_i, and μ_i as the mean calve production by females in stage *i* (hereafter referred as "fecundity" to differentiate from the "fertility" matrix element F_i). Then, the matrix elements P_i and G_i are defined as σ_i $(1- \gamma_i)$ and $\sigma_i\ \gamma_i$, respectively, where the term γ_i is the reciprocal of the stage duration. Only G_2 included an additional parameter to represent the proportions of juveniles transitioning into young reproductive females (φ_f) or young mature males (φ_m) as $G_{2\mathrm{f}} = \sigma_2\ \gamma_2\ \varphi_\mathrm{f}$ and $G_{2\mathrm{m}} = \sigma_2\ \gamma_2\ \varphi_\mathrm{m}$. These proportions were computed from the total number of 10-year old males or females during 1987-2011. A birth-flow matrix variant (Caswell 2001) was used because births occur essentially year-round, with $F_i = \sigma_1^{0.5}\left(\left(1+P_i\right)\mu_i + G_i\mu_{i+1}\right)/2$ and $G_1 = \sigma_1^{0.5}$, where σ_1 is the survival probability of calves and where F_2 represents the fecundity of those juvenile individuals that become young reproductive females during the projection interval (Brault & Caswell 1993, Crouse et al. 1987).

Since most births seem to occur between fall and spring (Bigg et al. 1990, Olesiuk et al. 1990) and most encounters (RKW sightings) occur during the summer months (Ford 2006), individuals encountered in the summer are assumed to be censused at the midpoint between birthdays. Thus, January 1st was used to determine stage affiliations in a given year and as the beginning of the projection interval. Based on census data, survival σ_i was computed as the number of individuals in stage *i* at year *t* surviving to year *t*+1. We did not base fecundity (μ_i) estimates on newborn individuals because not all killer whale births are observed, which means that pregnancy rates and birth rates are expected to be higher than the production of viable calves (see Olesiuk et al. 1990). Viable calves were defined as those individuals that survived to at least 0.5 years of age and fecundity μ_i was computed as the ratio of the number of viable calves produced by females in stage *i* at year *t* to the number of females in that stage and year. In this way, although neonate mortality is unknown, it is accounted for by the fecundity rate (see also Olesiuk et al. 1990). Thus, vital rate μ_i rightly represents the production of viable calves. And since individuals are censused at the midpoint between birthdays, viable calf survival refers to survival from 0.5 years to 1.5 years. Time series of RKW abundance and vital rates are summarized in Appendix B.

The matrix population model **M** corresponding to the stage-structured life cycle in Figure 2 is shown in Equation 1, where the upper left sub-matrix describes the production of juveniles and mature females by females, the lower left sub-matrix the production of mature males by females, the lower right sub-matrix the production of mature males by males, and the upper right sub-matrix the production of females by males. In Equation 1, $P_1 = 0$, because the length of the calf stage is equal to the projection interval (1 year). Life expectancy was computed from **M** following Caswell & Fujiwara (2004; see also Appendix C).

$$\mathbf{M} = \left(\begin{array}{ccccc|cc} 0 & F_2 & F_3 & F_4 & 0 & 0 & 0 \\ G_1 & P_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & G_{2f} & P_3 & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3 & P_4 & 0 & 0 & 0 \\ 0 & 0 & 0 & G_4 & P_5 & 0 & 0 \\ \hline 0 & G_{2m} & 0 & 0 & 0 & P_6 & 0 \\ 0 & 0 & 0 & 0 & 0 & G_6 & P_7 \end{array}\right) \tag{1}$$

2.3. Perturbation analysis

Demographic perturbation analysis was used in two distinct ways to study population responses to changes in the vital rates (Caswell 2001). Prospective analyses (sensitivity and elasticity) explored the functional dependence of λ on the vital rates (Brault & Caswell 1993, Fujiwara & Caswell 2001, Vélez-Espino & Koops 2009a) to predict the changes in λ that would result from any specified change in the vital rates; these changes are independent of previous patterns of variability in the vital rates. Changes in vital rates with high elasticity will produce large relative changes in λ (Vélez-Espino et al. 2006). The retrospective analysis relied on the random design methodology used for life table response experiments (Brault & Caswell 1993, Caswell 1989, Levin et al. 1996), which involves matrix construction breaking down the variance of λ into the contributions from the variances in the vital rates (see Table 2). Retrospective analyses cannot identify potential management targets because they compare the contributions of past changes in vital rates, not the effects of future changes (Bruna & Oli 2005, Caswell 2000, Cooch et al. 2001). We also computed variance-standardized elasticities, following Zuidema and Franco (2001), as the product of vital rate elasticities and vital rate temporal CV to generate the contribution of vital rate covariation on λ's coefficient of variation CV(λ). Appendix C contains additional detail on retrospective analyses.

The computation of sensitivities and elasticities as well as the decomposition of the variance in population growth, fundamental for prospective and retrospective analyses, has been detailed elsewhere (e.g., Caswell 2001). The equations involved in these analyses are summarized in Table 2, including the effect on λ of multiple perturbations (λ_{new}) and the proportional increase in a vital rate $\delta(v_i)$ necessary to achieve a target population growth rate.

Analytical solutions to prospective perturbations in Table 2 are robust for perturbations up to 30% and occasionally up to 50% (Caswell 2001). Nonlinearities, often exhibited between vital rates and λ (see de Kroon et al. 2000, Mills et al. 1999, Vélez-Espino 2005), reduce the accuracy of projections using elasticities for larger perturbations. Hence, we also conducted prospective perturbation analysis by directly perturbing the projection matrices (Ehrlén & van Groenendael 1998). Direct perturbations involve an iterative process, altering the magnitude of the vital rate in question while keeping all other matrix elements unchanged. In addition, because the ability to increase λ by improving individual vital rates will depend not only on the elasticities of survival or fecundity rates but also on the capacity to improve each vital rate (Morris & Doak 2002), we calculated the maximum proportional change in λ due to maximization of vital rates (Table 2). This is particularly important for RKW since annual survival rates have been estimated to be greater than 80% in most life stages and both sexes in SRKW (Krahn et al. 2004) and greater than 90% in NRKW (Olesiuk et al. 2005), thus leaving little room for improvement.

Stochastic versions of the population growth rate before and after exerted perturbations, elasticities, and the necessary increase in a vital rate that achieves a target population growth rate were generated through simulations with vital rates represented as random variables. The beta distribution was used to simulate variation in stage-specific survival (σ_i). This distribution is appropriate for survival as it produces random variables confined to the interval 0 to 1. The lognormal distribution was used to simulate fecundity values (μ_i). This distribution produces only positive random variables bounded by zero and infinity. Randomly sampled vital rates were used to generate 5000 random matrices, population growth rates and vital rate elasticities were calculated for each of these matrices, and a parametric bootstrap was used to estimate mean stochastic elasticities and their 95% confidence intervals.

2.4. Population Viability Analysis

We used projection matrices to conduct PVA under an independently and identically distributed (IID[2]) environment employing R software (R Development Core Team 2011) and in a fully stochastic fashion using $\text{RAMAS}_{\text{GIS}}$ (Akcakaya 2002). The two types of simulations were designed to contrast the importance of demographic and environmental stochasticity vs. IID environments on quasi-extinction, extinction, and recovery probabilities. For IID assessments, six matrices constructed with vital rates representative of four-year non-overlapping periods were randomly drawn to generate 5000 realizations of population growth to project future population size and compute stochastic population growth and 95% confidence intervals. The fraction of realizations hitting population size thresholds during or before a given time horizon was used to generate a cumulative distribution function and estimate quasi-extinction, extinction, and recovery probabilities. Initial conditions were represented by RKW stage compositions in 2011. Projections of population size were conducted at time horizons large enough for convergence to stable stage population structures (i.e., damping times; see Appendix C for additional detail).

For fully stochastic assessments, input data for RAMAS simulations consisted of a projection matrix of mean values and a corresponding matrix of standard deviations for each modeled RKW population. Mean and standard deviation matrices were constructed from the means and standard deviations of matrix elements from the six four-year matrices. RAMAS computer simulations consisted of 10,000 realizations of population size per time step from projection matrices with matrix-elements drawn from lognormal distributions parameterized by the mean and standard deviation matrices. Initial conditions were represented by RKW stage compositions in 2011. The probability of falling below a population threshold (quasi-extinction probability in RAMAS) was computed as the proportion of realizations of population size ≤ 30 individuals for SRKW and ≤ 250 for NRKW. Thirty individuals for SRKW was considered small enough for inbreeding depression, Allee effects, and exacerbated demographic stochasticity playing important roles on extinction dynamics (see Morris & Doak 2002). For NRKW, with a clearly positive population growth and 268 individuals in 2011, a threshold of 250 individuals was identified as useful for exploration of population viability metrics. Density dependence at high population size was not explicit in the RAMAS simulations given the paucity of information on carrying capacities for both RKW populations and the short time frames used for risk assessment. Demographic stochasticity, which is the temporal variation in

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[2] In probability theory and statistics, a sequence or other collection of random variables is independent and identically distributed (IID) if each random variable has the same probability distribution as the others and all are mutually independent. In the case of projection matrices, the IID concept entails the independence of individual period-specific matrices constructed with vital rates drawn from identical distributions in each case. Simulations based on projection matrices in an IID environment thus assume that past conditions apply to the future.

population growth driven by chance variation in the actual fates of different individuals within a year, was included in the RAMAS simulations (see Appendix C for details).

Interval extinction risk for both populations was computed as the probability that abundance will fall below a range of abundances at least once during the next 100 years. Probabilities of recovery in SRKW were computed using as population size targets 120 and 164 individuals as derived from an average growth of 2.3 percent per year for 14 years for downlisting and 28 years for delisting, respectively, specified in the recovery plan for this population (NMFS 2008). Lastly, expected minimum abundance for NRKW was calculated as the average (over all replications) of the minimum population abundance of the trajectory. The expected minimum abundance is used as an index of propensity to decline, especially useful when population variability and risks of decline are low (McCarthy & Thompson 2001).

3.0. RESULTS

3.1. Killer whale demography

Most vital rate mean values and distributions were relatively similar between SRKW and NRKW. Mean survival ranged from 0.785 (viable calf) to 0.985 (young reproductive female) in SRKW and from 0.883 (post-reproductive female) to 0.989 (young reproductive female) in NRKW. Mean fecundity was 0.116 and 0.069 in SRKW and 0.142 and 0.101 in NRKW for young reproductive females and old reproductive females, respectively. Nonetheless, viable calf survival and old-reproductive-female fecundity were significantly lower in SRKW (Nonparametric Kolmogorov-Smirnov test $p < 0.05$; Table 1). Viable calf survival rate in SRKW was effectively zero in 1988 and as low as 0.33 in 1999, 2006 and 2008, whereas the lowest viable calf survival in NRKW was 0.66 in 2000. In addition, there were no viable calves in SRKW for the 1996-1997 annual interval. If the net value of differences in vital rates between the two populations is added annually in a sequential fashion, the cumulative difference in viable calf survival stands out as the most important feature in favour of NRKW (Appendix D). Differences were not as marked for the fecundity of old reproductive females but there was a 5-year period, from 1997 to 2001, when SRKW's fecundity of old reproductive females was zero (Appendix B). In addition, the overall percentage of juveniles transitioning into young reproductive females from 1987 to 2011 was higher in NRKW (55%) than in SRKW (45%). This larger proportion of females partly explains NRKW's higher fecundity rates. Lastly, vital-rate coefficients of variation were greater for fecundity rates than for survival rates in both populations. Variation in vital rates was noticeably greater for all vital rates in SRKW than in NRKW, except for post-reproductive females (Table 1). There was generally low vital-rate covariation between populations.

Based on vital rates as random variables defined by their probability distributions (Appendix B), stochastic population growth rates were 0.91% annual decline ($\lambda = 0.9909$; 95% CI: 0.9719-1.0081) for SRKW and 1.58% annual increase ($\lambda = 1.0158$; 95% CI: 1.0027-1.0285) for NRKW (Figure 3). The current stage distribution of NRKW was closer to the stable stage distribution than it was for SRKW (Figure 4), with a noticeably higher proportion of post-reproductive females in SRKW than in NRKW (6.8% vs. 3.7%) and a higher proportion of juveniles in NRKW than in SRKW (34.8% vs. 27.3%). This difference also means that if current conditions persist (i.e., mean vital rates do not change), NRKW stage distributions would experience little change in the future while greater changes would likely occur for SRKW. SRKW's larger difference between observed and stable stage distribution also influenced this population's longer damping time (35 years for SRKW and 25 years for NRKW).

Mean life expectancies by life stage were longer for NRKW than for SRKW, except for post-reproductive females (Figure 5). Mean life expectancies of viable calves were 29.8 years for SRKW and 33.9 years for NRKW, slightly increasing for the juvenile stage to 32.5 years in SRKW and 34.3 years in NRKW. In both populations, an average young reproductive female had a mean life expectancy similar to that of viable calves whereas an average young mature male had a mean life expectancy that was about half of that estimated for viable calves in spite of the median age class being 21 years for young reproductive females and 16 for young mature males. Shorter life expectancies in males than females are a common pattern in cetaceans (Caswell & Fujiwara 2004).

There was a clear contrast between RKW vital rate elasticities, thus supporting the suitability of modeled life stages (Figure 6). The relative importance of individual vital rates on population growth rates (elasticity) was similar for both populations and it was greatest for the survival of young reproductive females (0.55 for SRKW and 0.53 for NRKW) and lowest for the fecundity of old reproductive females (0.009 for SRKW and 0.012 for NRKW). The elasticities of male survival and post-reproductive female are zero because these stages do not contribute directly to population growth. The elasticity of the proportion of juveniles transitioning into females was relatively small and comparable to that of viable calf survival (0.032 for SRKW and 0.044 for NRKW) in both populations.

Although any change in the survival of young reproductive females is expected to have the greatest relative effect on population growth (as determined by its elasticity), the little room for improvement in this vital rate limited the proportional increase in population growth achieved by maximizing the survival of young reproductive females. Greater proportional increases in population growth were achieved via maximization of fecundity rates (Figure 7), particularly the fecundity of young reproductive females. The maximization of this vital rate was projected to produce a 1.7% annual increase in SRKW, considerably less than the 2.3% U.S. downlisting recovery target. This difference means that the feasibility of meeting such a recovery target would require substantial and simultaneous increases in several vital rates and most likely including the fecundity of young reproductive females.

The relationship between elasticity and expected changes to population growth was also examined without the limitations to increase a given vital rate (as in the case of the already high survival rates) by analyzing the necessary change to halt population growth (i.e., $\lambda = 1.0$) in NRKW. Due to its largest elasticity, a small reduction (3.1%) in the survival of young reproductive females would be enough to halt NRKW's population growth. On the other hand, NRKW's positive population growth would not be halted even after canceling completely the fecundity of old reproductive females (Figure 8).

The retrospective perturbation analysis identified survival of young reproductive females (matrix element P_3) as the largest contributor to the variance in population growth λ for SRKW, and the fertility of young reproductive females (matrix element F_3) as the largest contributor for NRKW (Appendix E). Similarly, at the vital-rate level, the young-reproductive-female annual survival was the largest contributor to the CV in population growth for SRKW whereas the fecundity of young reproductive females was the largest contributor for NRKW (Figure 9). Thus, the survival of young reproductive females is not only the vital rate with the greatest potential to influence future population growth but also the vital rate that had the greatest influence on the population growth variance for SRKW. The combination of survival of young reproductive female's largest elasticity and larger temporal variability explains this vital rate's dominant contribution to SRKW's population growth variance. This vital rate was near to constant in NRKW (CV = 1.24%) during 1987-2011.

3.2. Future population dynamics

3.2.1. SRKW status-quo conditions

Under status-quo conditions, SRKW's expected population size was 84 in 10 years, 78 in 20 years, 71 in 30 years, and 68 in 35 years (Figure 10; upper panel), with 35 years as the damping time for SRKW. Only a small fraction of the realizations of population size exceeded the initial population size (N = 88) at 10 and 20 years but at 35 years all realizations of population size were below 88 and some were as low as 55-60. Projections of population size under demographic stochasticity showed that the probability of falling below 30 individuals can be greater than zero at about 55 years in the future (Figure 11). However, the incorporation of both environmental and demographic stochasticity produced a probability trajectory where the probability of falling below 30 individuals was greater than zero at 10 years, 0.5 at 47 years and approximately 0.8 at 100 years (Figure 12; upper panel). In an IID environment and without demographic stochasticity, the probability of falling below 30 individuals remained effectively zero for about 80 years, after which the probability increased rapidly reaching 0.5 at about 130 years (Figure 12; upper panel), thus demonstrating the importance of incorporating demographic stochasticity in PVAs for a population with such small population size. But even without the inclusion of demographic stochasticity, there was a zero probability of SRKW reaching 120 individuals in 14 years corresponding to the U.S. downlisting target. Moreover, when the time horizon is fixed, rather than fixing the population threshold, there was an extinction risk of 49% in 100 years (Figure 12; lower panel) and an expected minimum abundance of 15 individuals during this timeframe.

3.2.2. NRKW status-quo conditions

Under status-quo conditions, and in the absence of density dependence, NRKW's expected population size was 315 in 10 years, 370 in 20 years, 401 in 25 years, and 434 in 30 years (Figure 10; lower panel) with 25 years as the damping time for NRKW. No realizations of population size were smaller than the initial population size (N = 268) at 10 years, and at 25 years some realizations of population size were as high as 480 individuals. In an IID environment and without demographic stochasticity, the probability of falling below 250 individuals remained effectively zero even after 250 years (no figure shown). However, projections of population size under demographic stochasticity showed steadily increasing trajectories and no trajectory falling below 250 individuals (Figure 11). The incorporation of both environmental and demographic stochasticity produced a rapidly increasing probability trajectory where the probability of falling below 250 individuals was 0.5 at 30 years, and asymptotically reached 0.52 after 100 years (Figure 12; upper panel). This pattern is different to the probability trajectory for SRKW mainly due to the clearly positive population growth exhibited by NRKW. When the time horizon is fixed, rather than fixing the population threshold, there was an extinction risk of zero in 100 years (Figure 12; lower panel) and an expected minimum abundance of 238 individuals during this timeframe.

3.3. Viability responses to perturbations on vital rates

We analyzed the responses of extinction probabilities to perturbations (positive perturbations for SRKW and negative for NRKW) on those vital rates identified as significantly different between resident killer whale populations (i.e., viable calf survival and fecundity of old reproductive females) and on those vital rates with the largest influence on population growth (fecundity of young reproductive females for SRKW and the survival of young reproductive females for NRKW).

Increasing viable calf survival in SRKW produced a quasi-linear decline in mean extinction risk in 100 years from 49.2% (PVA with no perturbation) to a minimum of 35.4%. This minimum was produced by a positive perturbation of 37% corresponding to vital rate maximization (Figure 13a). Relative to status-quo conditions, SRKW's stochastic population growth rate increased as a result of this positive perturbation but it remained slightly negative at a 0.16% annual decline (λ = 0.9984; 95% CI: 0.9796-1.0153). Decreasing viable calf survival in NRKW to a maximum level of 37%, mirroring the maximum increase in this vital rate for SRKW, increased extinction risk in 100 years from 0% (PVA with no perturbation) to only 2.9%. NRKW's stochastic population growth was effectively halted after an average 34.2% decrease in viable calf survival, and it became slightly negative (λ = 0.9987; 95% CI: 0.9873-1.0092) at a 37% decrease.

Positive perturbations in SRKW's fecundity of old reproductive females were much larger than those for viable calf survival given their substantially larger room for improvement allowing a maximum increase of 275% in this vital rate. The feasibility of increasing this vital rate to such levels produced a linear decline in extinction risk in 100 years down to 26.3% at about a 175% increase in the fecundity of old reproductive females, slowing down after that to reach a minimum mean extinction risk in 100 years of 23.5% (Figure 13b). SRKW's mean stochastic population growth rate became positive as a result of the maximum positive perturbation in this vital rate, reaching a 0.50% annual increase (λ = 1.0050; 95% CI: 0.9842-1.0264). Decreasing NRKW's fecundity of old reproductive females down to zero increased extinction risk in 100 years to only 3.6%. The total cancelation of this vital rate did not halt NRKW's stochastic population growth, which remained slightly positive (λ = 1.0016; 95% CI: 0.9879-1.0149).

Positive and identical perturbations to SRKW's viable calf survival and fecundity of old reproductive females to a maximum level of 37% (maximum average increase for viable calf survival) produced a quasi-linear decline in mean extinction risk in 100 years to a minimum of 29.9%, which was not markedly different from the minimum extinction risk produced by the maximization of viable calf survival alone (Figure 13c). SRKW's mean stochastic population growth rate became positive as a result of these positive perturbations in these vital rates, reaching 0.81% annual increase (λ = 1.0081; 95% CI: 0.9883-1.0275), which was slightly greater than the stochastic growth achieved through maximization of fecundity of old reproductive females alone. For NRKW, simultaneous negative perturbations on calf survival and fecundity of old reproductive females to a maximum level of 37%, mirroring the maximum simultaneous increase in these vital rates for SRKW, increased extinction risk in 100 years to 6.5%, which was about twice the extinction risk produced by either the minimization of viable calf survival or the cancelation of fecundity of old reproductive females. NRKW's stochastic population growth was effectively halted after an average 27.5% simultaneous decrease in both vital rates, and it became slightly negative (λ = 0.9945; 95% CI: 0.9838-1.0049) after a 37% simultaneous decrease in these vital rates. This stochastic population growth was not markedly different from that achieved through the minimization of viable calf survival alone.

The vital rate with the greatest potential to exert positive changes in SRKW's population growth was clearly the fecundity of young reproductive females (Figure 7). The maximum feasible increase to this vital rate was 206%, which was not as high as that for the fecundity of old reproductive females but had a greater potential to increase SRKW's population growth due to its greater elasticity (Figure 6). Linear decreases in extinction risk in 100 years down to 22.9% were achieved at about a 75% increase in the fecundity of young reproductive females, slowing down after that to reach a minimum mean extinction risk in 100 years of 13.4% (Figure 13d). The maximization of this vital rate produced a clearly positive mean stochastic population growth indicating a 1.79% annual increase (λ = 1.0179; 95% CI: 0.9989-1.0367).

In the case of NRKW, the vital rate with the greatest potential to exert negative changes in this population's growth rate was clearly the survival of young reproductive females (Figure 8). Steep linear increases in NRKW's extinction risk resulted from reductions in this vital rate as large as 25%, and mean population growth rate was effectively halted after only a 3.1% decrease in this vital rate. The increase in extinction risk slowed down at larger negative perturbations, achieving a maximum extinction risk in 100 years of 94.5% after bringing the survival of young reproductive females down to zero. In this case, the time horizon of 100 years is evidently limiting the propagation of extinction risk to 100% since zero survival of young reproductive females would eventually lead to certain extinction.

4.0. DISCUSSION

4.1. Demographic differences between SRKW and NRKW

Our investigation revealed four main demographic factors that explain SRKW's lower population growth and viability relative to NRKW. The survival of viable calves and the fecundity of old reproductive females have been significantly lower in SRKW than in NRKW. Although not significantly greater, the cumulative annual differences between populations in the survival of post-reproductive females is the only vital rate standing out in favour of SRKW (Appendix D). However, this vital rate does not contribute directly to population growth rate. Interestingly, a recent study found that the presence of post-reproductive females seems to substantially increase the survival probabilities of their sons older than 30 (Foster et al. 2012).

A third factor contributing to the lower population growth rate of SRKW relative to NRKW is SRKW's lower proportion of juveniles transitioning into young reproductive females. Although the departures from a balanced sex ratio are small in both populations, they are significantly positive for NRKW (+5%) and negative (-5%) for SRKW, for a total difference of 10% in this parameter in favour of NRKW. The proportion of females, φ_f, not only contributes to the stage-transition probabilities but also to fecundity rates. Sex ratio has a significant effect on a population's ability to increase from low numbers, and this ability is enhanced when females predominate and is depressed when males dominate (Caughley 1994). One of the advantages of our two-sex model was that the relative influence of the sex ratio of mature individuals (i.e., proportion of reproductive females) on population growth can be quantified using elasticity analysis.

Lastly, SRKW's greater vital rate variances emerged as a fourth demographic factor explaining the lower population viability of this population. Temporal variation in vital rates was noticeably greater in SRKW than in NRKW, except for the survival of post-reproductive females. This difference is important because the demographic viability of a population will be mainly determined by its capacity to increase from low numbers and its ability to buffer both density-dependent and environmentally-driven variability in its vital rates (Vélez-Espino & Koops 2012). Density-driven vital rate variability can be linked to SRKW's small population size. There is evidence that inter-annual variability in survival in some vertebrate taxa increases at low abundance in an inverse density-dependent fashion and that this relationship has important consequences for recovery and population persistence (Minto et al. 2008). This greater variability in vital rates could be also associated with demographic stochasticity, which our analyses demonstrated has a strong negative influence on SRKW's projections of population size. The influence of demographic stochasticity on population dynamics is inversely related to population size, it can create substantial variability at low population sizes, and it can translate into greater extinction risk (Morris & Doak 2002).

The foregoing discussion identified those demographic factors driving the lower population performance of SRKW relative to that of NRKW. However, the factors underpinning the lower fecundity and survival of viable calves in SRKW have not been identified and they could be environmental, anthropogenic or genetic. Ford et al. (2011) found no evidence of offspring produced by close relatives but found instead evidence of inbreeding avoidance in SRKW, which has been also observed in other killer whale populations (e.g., Barrett-Lennard 2000). It is therefore possible that inbreeding avoidance in a small population such as SRKW can be a deterrent for reproductive opportunities and ultimately a limiting factor for pregnancy and fecundity rates.

Among the environmental factors, the availability of Chinook salmon (*Oncorhynchus tshawytscha*), which is predominant item in RKW's diet (Ford et al. 2010a, Hanson et al. 2010), has been identified as a potential limiting factor to RKW's population dynamics (COSEWIC 2008, Ford et al. 2010b). In a recent study, Vélez-Espino et al. (2013) found numerous interactions between Chinook abundance aggregates and RKW vital rates but no evidence of differences in viable calf survival or old-reproductive-female fecundity between NRKW and SRKW resulting from different interaction levels with Chinook salmon resources or associated to trends in the abundance of Chinook stocks identified as relevant in their diets. The possibility of territoriality taking place between SRKW and NRKW and suppressing feeding rates of SRKW on common prey resources based on NRKW's higher abundance cannot be discounted. However, there is no evidence of territoriality in resident killer whales (Ford et al. 2000) or cetaceans in general (Mann et al. 2000).

In addition to nutritional stress linked to prey availability, other factors that have been associated with the poor status of SRKW include effects of exposure to pollutants (particularly PCBs and PBDEs; Krahn et al. 2007) and disturbance from boat traffic (Lusseau et al. 2009, Williams et al. 2009) on RKW's vital rates. Unlike NRKW, SRKW resides in a more urbanized environment and therefore this population is more exposed to boat disturbance and environmental contaminants (Krahn et al. 2002). However, direct links between anthropogenic factors and RKW demographic rates are difficult to measure. The population effects of the live captures for the aquaria trade are an exception. This fishery caused a large reduction in population size and disruption of stage structures of both RKW populations, particularly SRKW. Olesiuk et al. (1990) estimated that 93% of the killer whales cropped between 1962 and 1977 were RKW and that 76% of these were taken from SRKW. Although the influence of this perturbation on population structure vanished by the early 1990's, some of the early years in our study period would have been influenced by this anthropogenic factor. Low calving rates in SRKW during the years after cropping ended could be partly explained by a reduction in the number of mature males below a critical number for optimal productivity (Olesiuk et al. 1990). Currently, the proportions of mature males in the population (22.7% in SRKW and 21.1% in NRKW) and the sex ratios (~ 0.6:0.4 female-to-male) are similar between these two populations.

4.2. Population Viability Analysis

4.2.1. Projected dynamics under status-quo conditions

It should be strongly emphasized that the purpose of a PVA is not to make predictions of future population state since there will always be unforeseen sources of uncertainty. Our projections indicate that if the means and variances of SRKW's vital rates remain at levels observed for 1987-2011, a stable stage distribution could be reached after 35 years at a mean population size of 68 individuals. Demographic stochasticity could be exacerbated as population size decreases, thus increasing the risk of entering an extinction vortex where genetic factors and Allee effects[3] (Dennis 1989, 2002, Philip & Sutherland 1999) could

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[3] Allee effects encompass any mechanism of beneficial effects of conspecific presence (e.g., reduction of inbreeding and genetic drift, social facilitation for reproduction, etc.) that leads to positive relationships

accelerate rates of decline (Gilpin & Soulé 1986). Hence, projections of declines to quasi-extinction thresholds are deemed as more robust than projections of declines to actual extinction because the latter could be characterized by a vortex of increasing variability and increasing rates of decline (Fagan & Holmes 2006). The inclusion of demographic stochasticity in our fully-stochastic simulations accounted for some of this additional variability in population size at low abundance. Nevertheless, our actual-extinction probabilities ($N = 0$) are rather conservative since an increasing vital rate variability and an increasing role of Allee effects at low population size were not incorporated in the simulations. Other factors not included in our PVA that have the potential to increase extinction probabilities and diminish projected population sizes could include climate change, catastrophes, and loss of fitness due to genetic stochasticity (Lande 2002). Population viability could be more pessimistic if catastrophes are included given the large effects catastrophes can have on PVAs (Lande 1993, Menges 1990, Mangel & Tier 1994, Vélez-Espino & Koops 2012).

In the case of NRKW, which has a maximum 52% risk of falling below 250 individuals and a zero probability of actual extinction in 100 years, the main limiting factor for projections of population size would be the carrying capacity of the system, which is an unknown parameter. In the absence of density dependence, and if means and variances of NRKW's vital rates remain at levels observed for 1987-2011, a stable stage distribution could be reached after 25 years at a mean population size of about 400 individuals. Presently, demographic stochasticity has a smaller influence on NRKW's future population dynamics than on SRKW, and with clearly positive observed and projected population growth rates and larger population size, NRKW dynamics are expected to be relatively resilient to the potentially negative influence of amplified vital rate variability, Allee effects, and genetic factors associated to smaller populations.

4.2.2. Perturbations and PVA

The maximization of those vital rates identified as significantly different between the two populations, viable calf survival and fecundity of old reproductive females, produced slightly positive mean population growth rates and substantially reduced SRKW's extinction risk but not to the status-quo levels projected for NRKW. Accordingly, SRKW's stochastic population growth remained lower and extinction risk remained higher than in NRKW even after maximizing these vital rates due to the substantially larger temporal variability in SRKW's remaining vital rates. The coefficients of variation of SRKW's vital rates directly contributing to population growth were at least twice as large as those of NRKW. There is empirical and theoretical evidence indicating a positive relationship between population variability and extinction risk (Vucetich et al. 2000). Both the

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between a component of fitness (e.g., reproduction, survival, intrinsic rate of increase) and densities (Courchamp et al. 1999, Vélez-Espino & Fox 2005).

variability in a vital rate and its relative contribution to population growth determine its influence on population viability (Vélez-Espino & Koops 2012). Any projected trajectories of population size depend not only on the schedule of vital rates, but also on the variance in these rates mainly because variation in vital rates creates disequilibrium in age structure that further complicates the dynamics. The variance in stochastic population growth rates is thus attributable to both the variation in vital rates and the variance in population structure (Boyce 1992).

4.3. Final remarks

Our analyses indicate that the future demographic sustainability of SRKW is compromised by its small population size and slightly negative expected population growth. SRKW's slightly negative mean expected population growth derived from demographic projections is consistent with the count-based dynamics and rates of change observed during the last RKW generation. Past population dynamics of SRKW have been characterized by long-term realized population growth rates that consistently include negative lower bounds (Appendix F). The lower 95% confidence limit for SRKW's realized population growth was consistently negative during 1974-2011 and as low as -2.5% whereas for NRKW it was positive in most years (Figure F1).

In addition to SRKW's lower fecundity and survival of viable calves, greater variation in vital rates and a strong influence of demographic stochasticity on future population dynamics were identified as important factors contributing to SRKW's lower population viability. Since SRKW's vital rate variability is deemed as strongly related to its low population size, it is recommended to invest future research efforts identifying the causes of depressed fecundity and survival of viable calves as a first step towards the design and implementation of conservation actions directed to increasing population growth and reducing SRKW's vulnerability to demographic and environmental stochasticity.

Small reductions (~ 3%) in the survival of young reproductive females are enough to halt NRKW's population growth, stressing the relative vulnerability of this population. In general, any anthropogenic or environmental factors negatively affecting this vital rate are expected to have substantial detrimental effects on the dynamics of both resident killer whale populations. We also showed that in spite of the survival of young reproductive females having the largest elasticity in both populations, increasing this vital rate has a limited positive effect on RKW population growth given the little room to improve this vital rate. Management actions designed to increase the fecundity of young reproductive females are expected to have the largest positive effect on SRKW's population growth thus producing the largest reductions in extinction risk.

Finally, the U.S. downlisting recovery target of 2.3% annual growth rate for 14 years for SRKW seems biologically unfeasible. A pragmatic population growth-based recovery target for SRKW should not exceed the expected population growth for NRKW (1.58% annual growth). At any rate, if recovery takes place, long-term population growth is expected to be low. Deterministically, SRKW's could reach ~ 113 individuals in a generation (roughly one extra individual each year) under a feasible 1.0% annual growth rate.

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7.0. TABLES

Table 1. Vital rate and abundance statistics for resident SRKW and NRKW (1987-2011), their correlation coefficients, and statistical significance based on nonparametric Kolmogorov-Smirnov test comparing means and distributions of vital rates and abundance between these two populations: (*) $p < 0.05$; (**) $p < 0.01$; (***) $p < 0.001$.

	Mean		**SD**		**CV**			**Significantly**
Vital rate, Abundance	**SRKW**	**NRKW**	**SRKW**	**NRKW**	**SRKW**	**NRKW**	**Pearson r**	**different**
Calf Survival	0.7847	0.9218	0.2844	0.0882	36.24%	9.56%	0.338	**
Juvenile Survival	0.9807	0.9717	0.0466	0.0186	4.75%	1.91%	0.346	
Female 1 Survival	0.9846	0.9890	0.0333	0.0123	3.38%	1.24%	-0.042	
Female 2 Survival	0.9668	0.9826	0.0542	0.0253	5.60%	2.57%	-0.020	
Female 3 Survival	0.9278	0.8835	0.1076	0.1136	11.59%	12.86%	-0.029	
Male 1 Survival	0.9691	0.9771	0.0649	0.0276	6.70%	2.83%	-0.200	
Male 2 Survival	0.8972	0.9249	0.1446	0.0780	16.12%	8.43%	0.450	
Female 1 Fecundity	0.1163	0.1423	0.0766	0.0456	65.84%	32.01%	-0.236	
Female 2 Fecundity	0.0694	0.1008	0.0742	0.0512	106.94%	50.81%	0.260	*
Abundance	88	217	4.8261	25.7792	5.49%	11.89%	0.117	***

Table 2. Summary of equations and definitions for demographic rates used in prospective and retrospective perturbation analyses.

Perturbation type	Demographic rate	Computation	Definitions
Prospective	Matrix element elasticity	$\varepsilon\left(a_{kl}\right) = \partial \log \lambda / \partial \log a_{kl}$	a_{kl} : individual matrix element
	Vital rate elasticity	$\varepsilon\left(v_i\right) = \frac{v_i}{\lambda}\frac{\partial \lambda}{\partial v_i} = \frac{v_i}{\lambda}\sum \frac{\partial \lambda}{\partial a_{kl}}\frac{\partial a_{kl}}{\partial v_i}$	v_i : vital rate
	Effect of multiple perturbations on λ	$\lambda_{new} = \lambda\left(1+\sum \varepsilon\left(v_i\right)\cdot\delta\left(v_i\right)\right)$	$\delta(v_i)$: proportional change in vital rate
	Necessary vital rate change to achieve a target λ	$\delta\left(v_i\right) = \left(\frac{1}{\sum \varepsilon\left(v_i\right)}\right)\left(\frac{\lambda_{\mathrm{target}} - \lambda}{\lambda}\right)$	$\lambda_{\mathrm{target}}$: desirable population growth rate
	Maximum proportional change in λ	$\Delta\lambda_{max}/\lambda \approx \sum\left(\varepsilon\left(v_{i,max} - v_i\right)/v_i\right)$	$v_{i,max}$: maximum vital rate value
Retrospective	Ccontributions of matrix elements to the variance in λ	$\mathrm{V}\left(\lambda\right) \approx \sum_{ij}\sum_{kl} \mathrm{s}_{ij}\mathrm{s}_{kl}\mathrm{C}\left(a_{ij}a_{kl}\right)$	s: matrix element sensitivity C: matrix element covariance
	Vital rate contributions to the variance in λ	$\mathrm{V}\left(\lambda\right) \approx \sum_{ij} \mathrm{C}\left(p_i, p_j\right)\frac{\partial \lambda}{\partial p_i}\frac{\partial \lambda}{\partial p_j}$	(p_i, p_j): vital rate pair extracted from population vectors **p**
	Matrix element sensitivity	$\partial\lambda/\partial a_{kl} = \left(\mathrm{v}_k \mathrm{w}_l\right) / \left\langle \mathbf{w},\mathbf{v} \right\rangle$	$\langle \mathbf{w},\mathbf{v} \rangle$: scalar product of the eigenvectors **w**: stable stage distribution **v**: reproductive value
	Simple vital rate contributions to coefficient of variation in λ	$\mathrm{CV}(\lambda)_i = \varepsilon(v_i)\ \mathrm{CV}(v_i)$	$\mathrm{CV}(v_i)$: temporal vital rate coefficient of variation

8.0. FIGURES

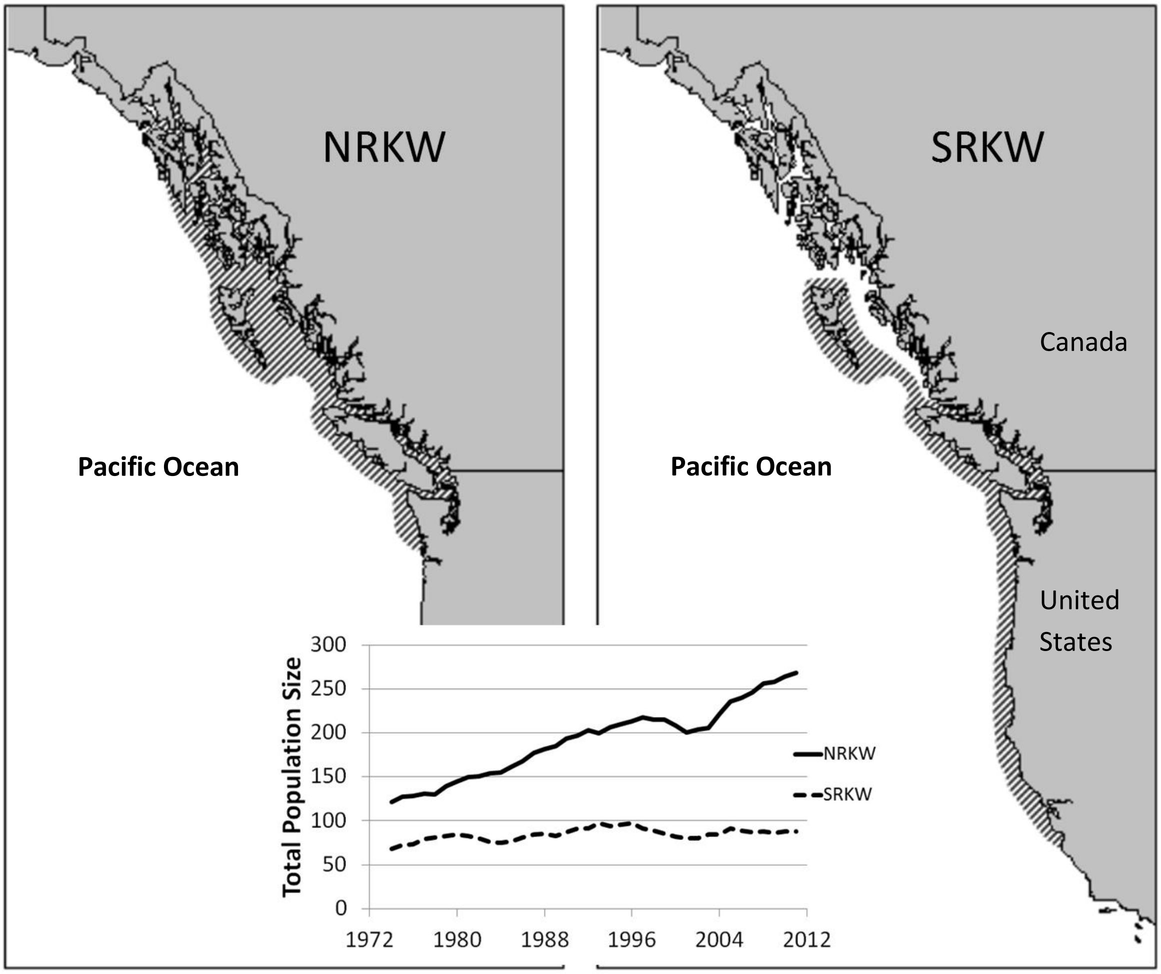


Figure 1. Known geographical ranges and population trends of northern (left) and southern (right) resident killer whales.

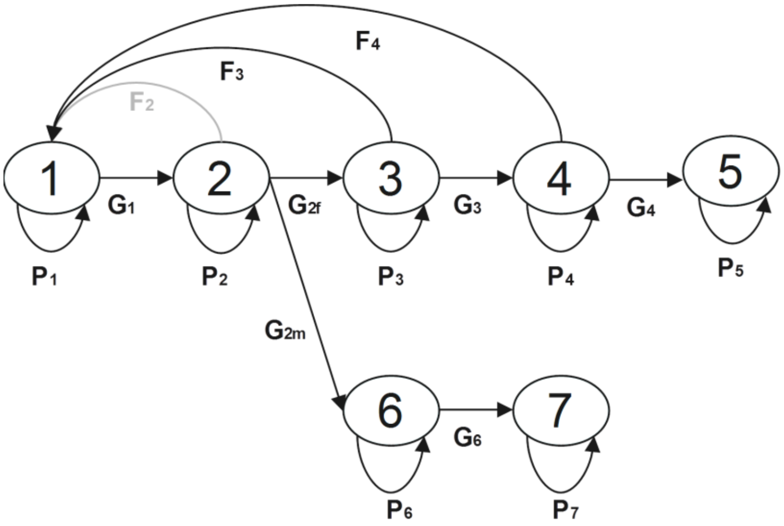


Figure 2. Stage-structured life cycle of resident killer whales with seven life stages: (1) calves; (2) juveniles; (3) young reproductive females; (4) old reproductive females; (5) post-reproductive females; (6) young mature males; and (7) old mature males. F_i represent fertility; G_i represent stage transition probabilities, with female and male juvenile-to-adult transitions indicated as G_{2f} and G_{2m}, respectively; and, P_i represent the probability of surviving and remaining in stage *i*.

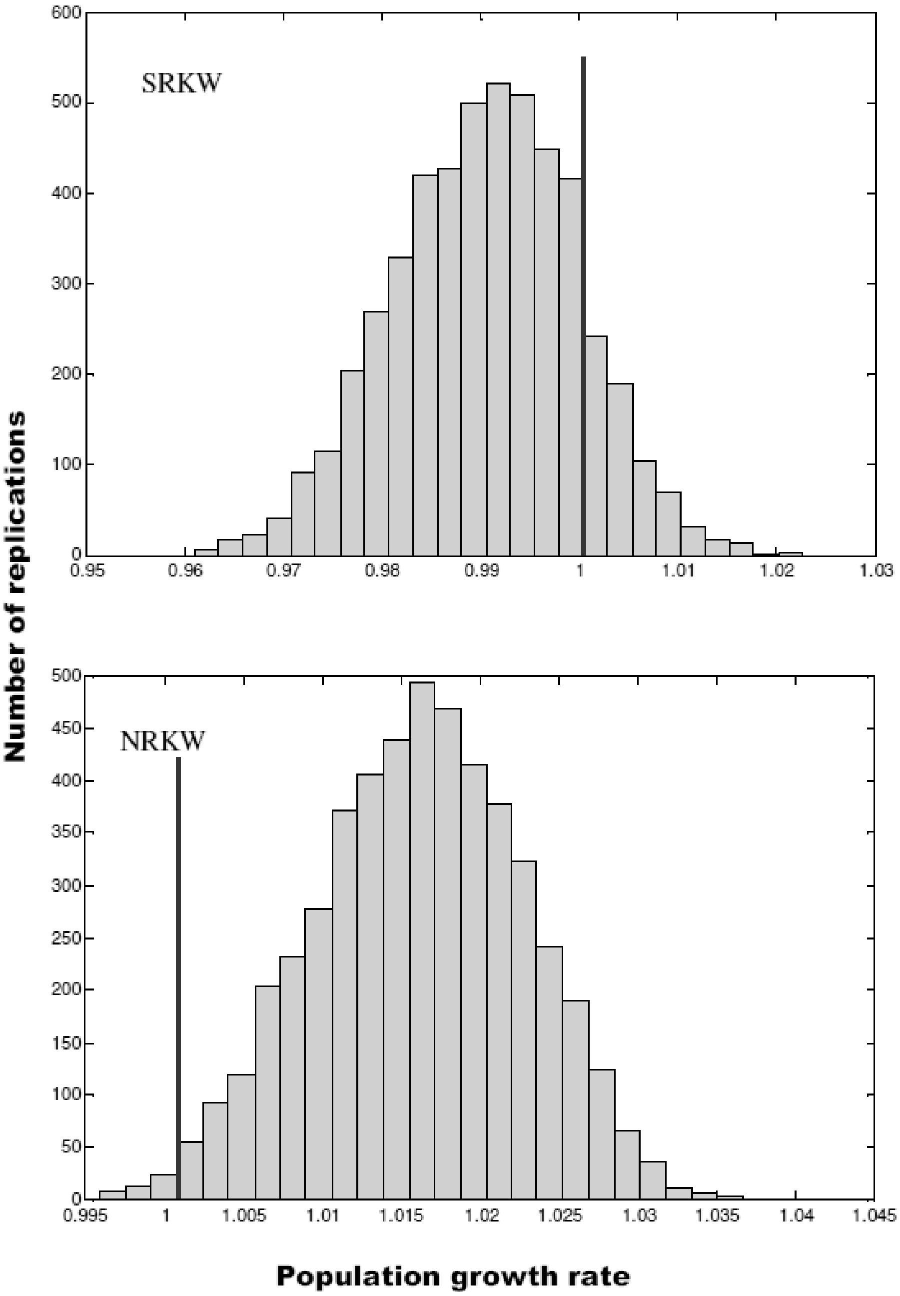


Figure 3. Frequency distribution of stochastic population growth computed through simulations (5000 replicates) for SRKW and NRKW. Vertical lines represent equilibrium ($\lambda = 1.000$).

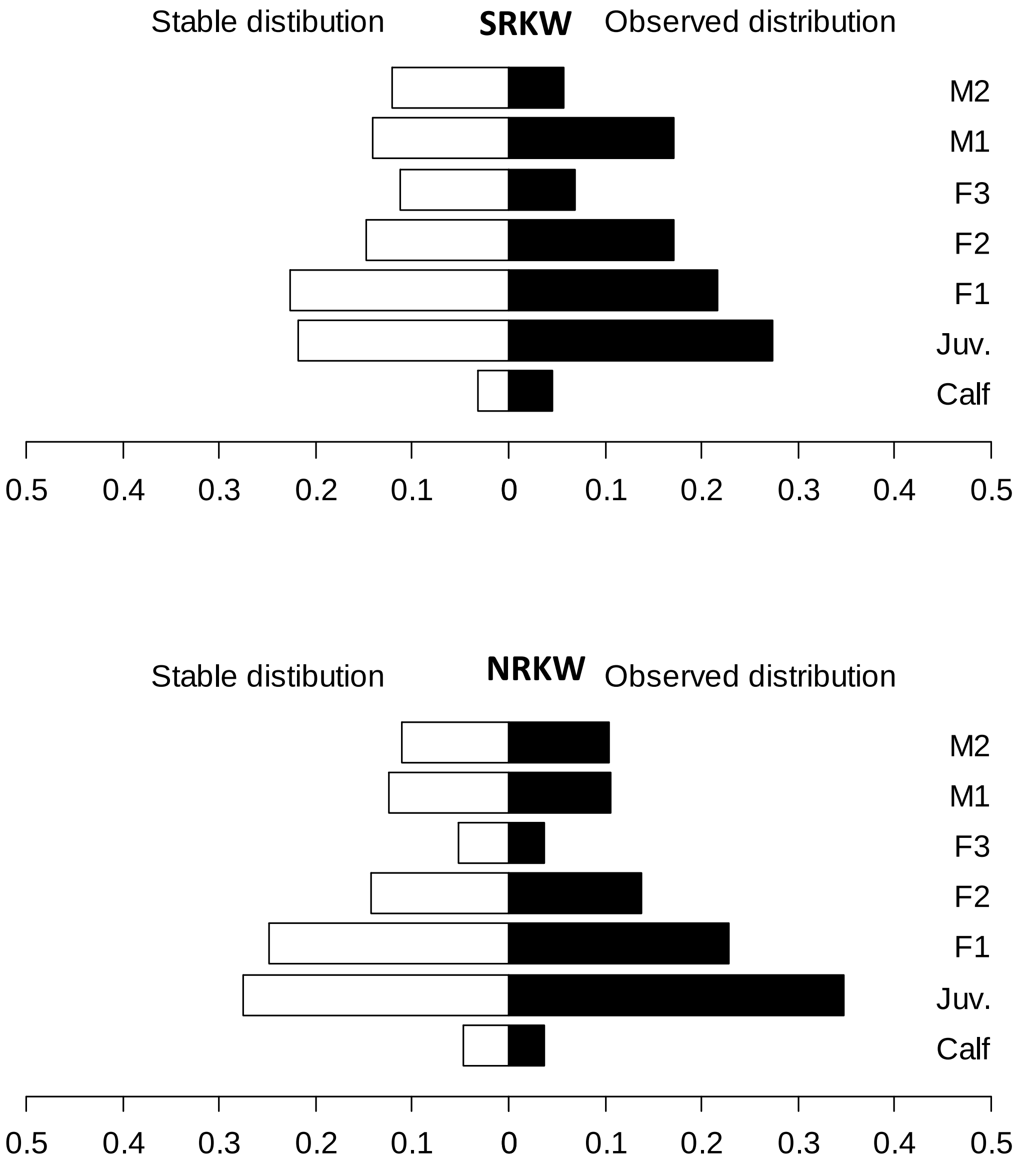


Figure 4. Comparison of stable stage distributions and observed stage distributions for SRKW (upper panel) and NRKW (lower panel). Juv.: Juvenile; F1: young reproductive female; F2: old reproductive female; F3: post-reproductive female; M1: young male; M2: old male.

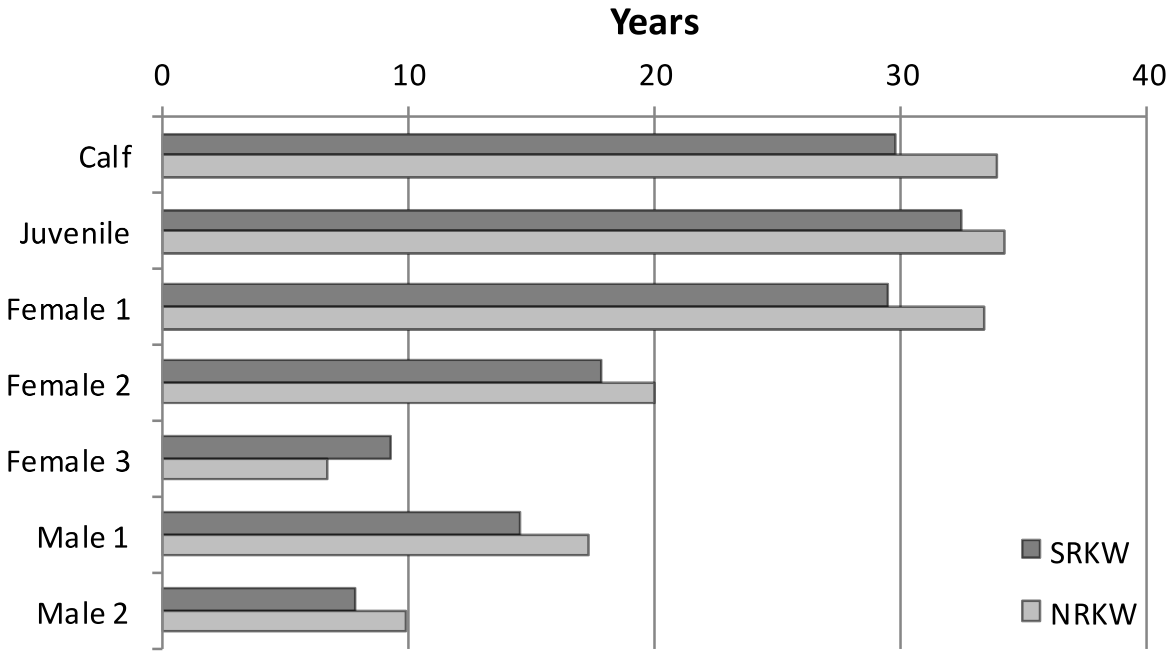


Figure 5. Mean life expectancy by life stage in SRKW and NRKW. Female 1: young reproductive female; Female 2: old reproductive female; Female 3: post-reproductive female; Male 1: young mature male; Male 2: old mature male.

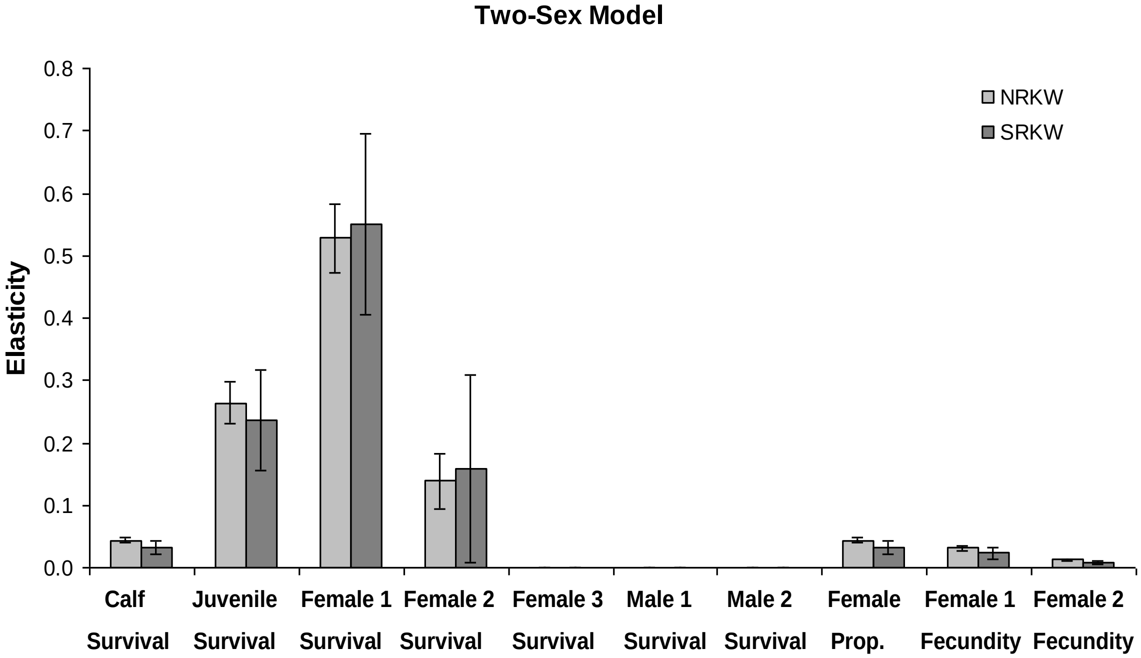


Figure 6. Stochastic vital-rate elasticities for NRKW and SRKW. Bars represent standard deviations. Female 1: young reproductive female; Female 2: old reproductive female; Female 3: post-reproductive female; Male 1: young mature male; Male 2: old mature male. The proportion of juveniles transitioning into young reproductive females is also included.

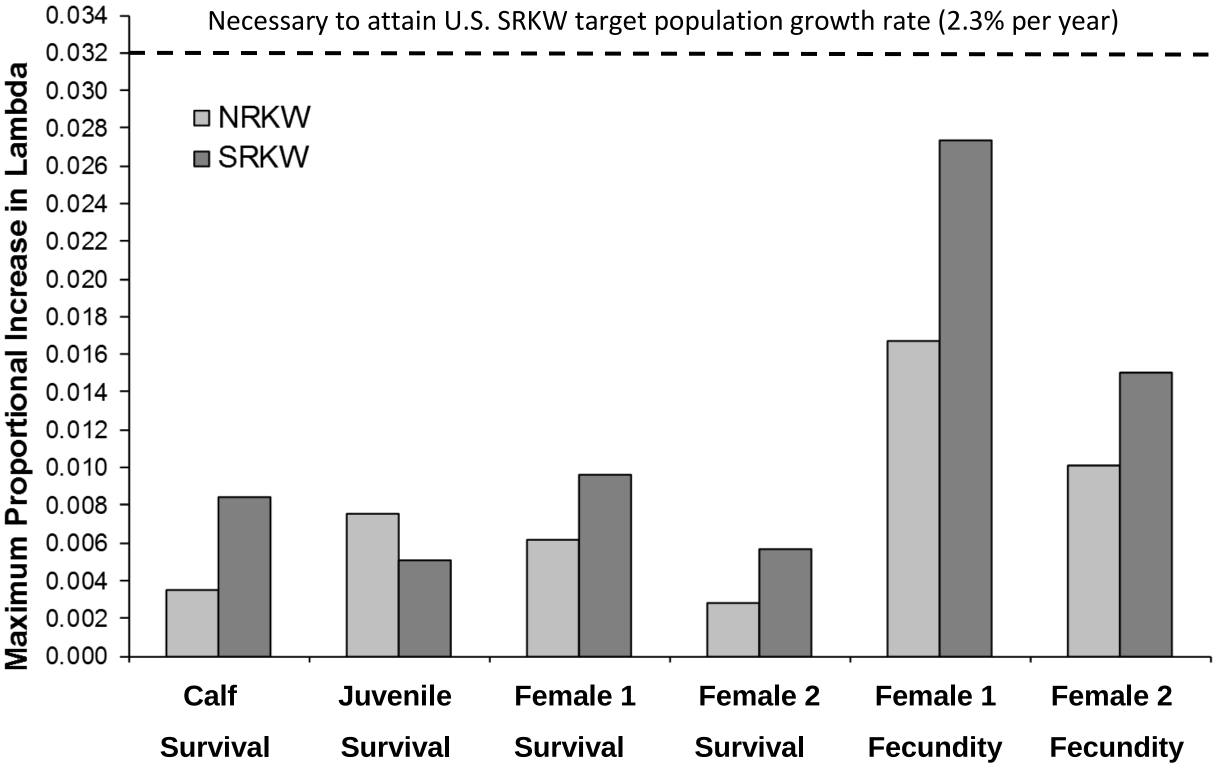


Figure 7. Maximum proportional increase in deterministic population growth resulting from maximization of individual vital rates (1.0 for survival and upper 95% C.L. for fecundity) in NRKW and SRKW. The proportional increase necessary to achieve the U.S. downlisting recovery goal is also shown. Female 1: young reproductive female; Female 2: old reproductive female.

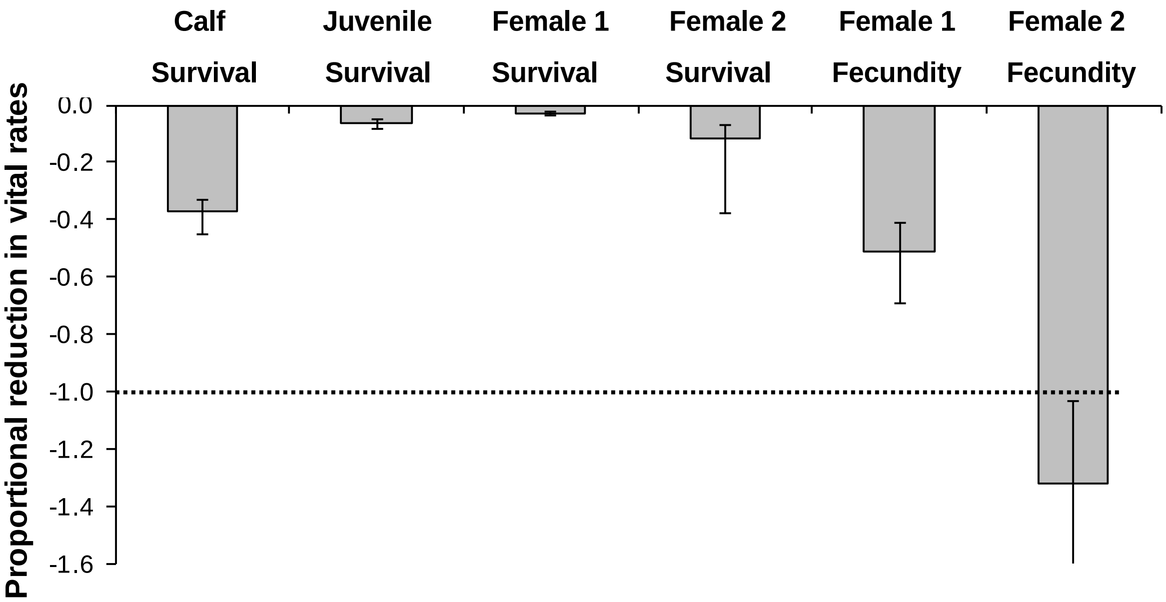


Figure 8. Proportional reduction in individual vital rates required to halt population growth (i.e., λ = 1.0) in NRKW. The horizontal line shows the maximum reduction in a vital rate. Female 1: young reproductive female; Female 2: old reproductive female. Bars represent 95% CIs.

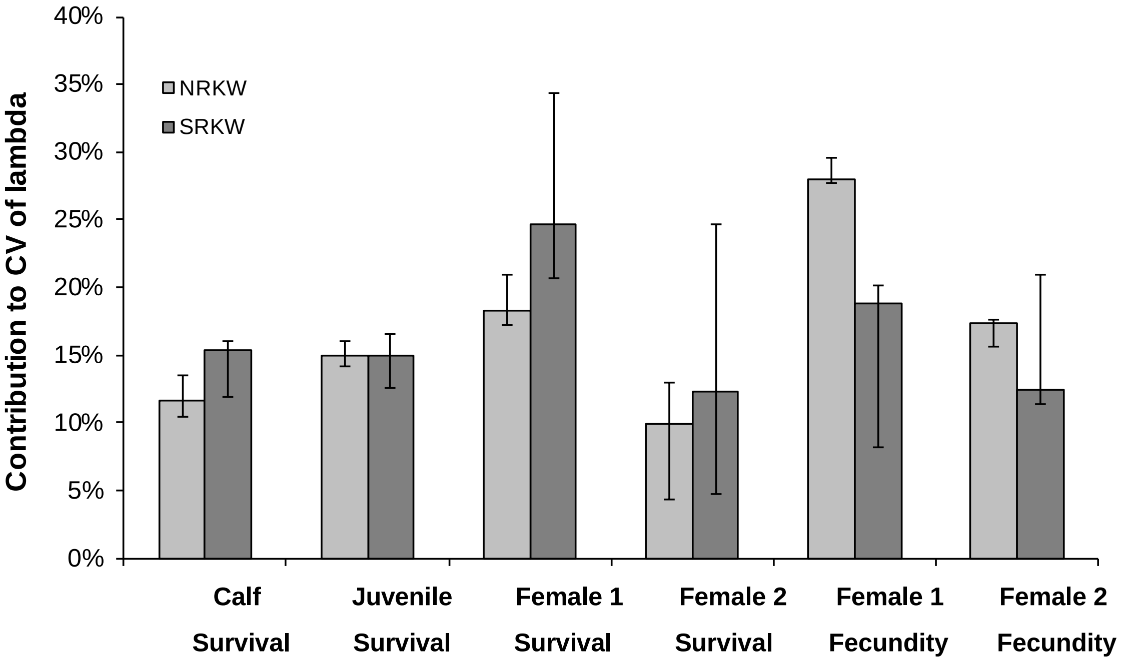


Figure 9. Stochastic contributions of individual vital rates to the CV in observed population growth for 1987-2011. Female 1: young reproductive female; Female 2: old reproductive female. Bars represent 95% CIs.

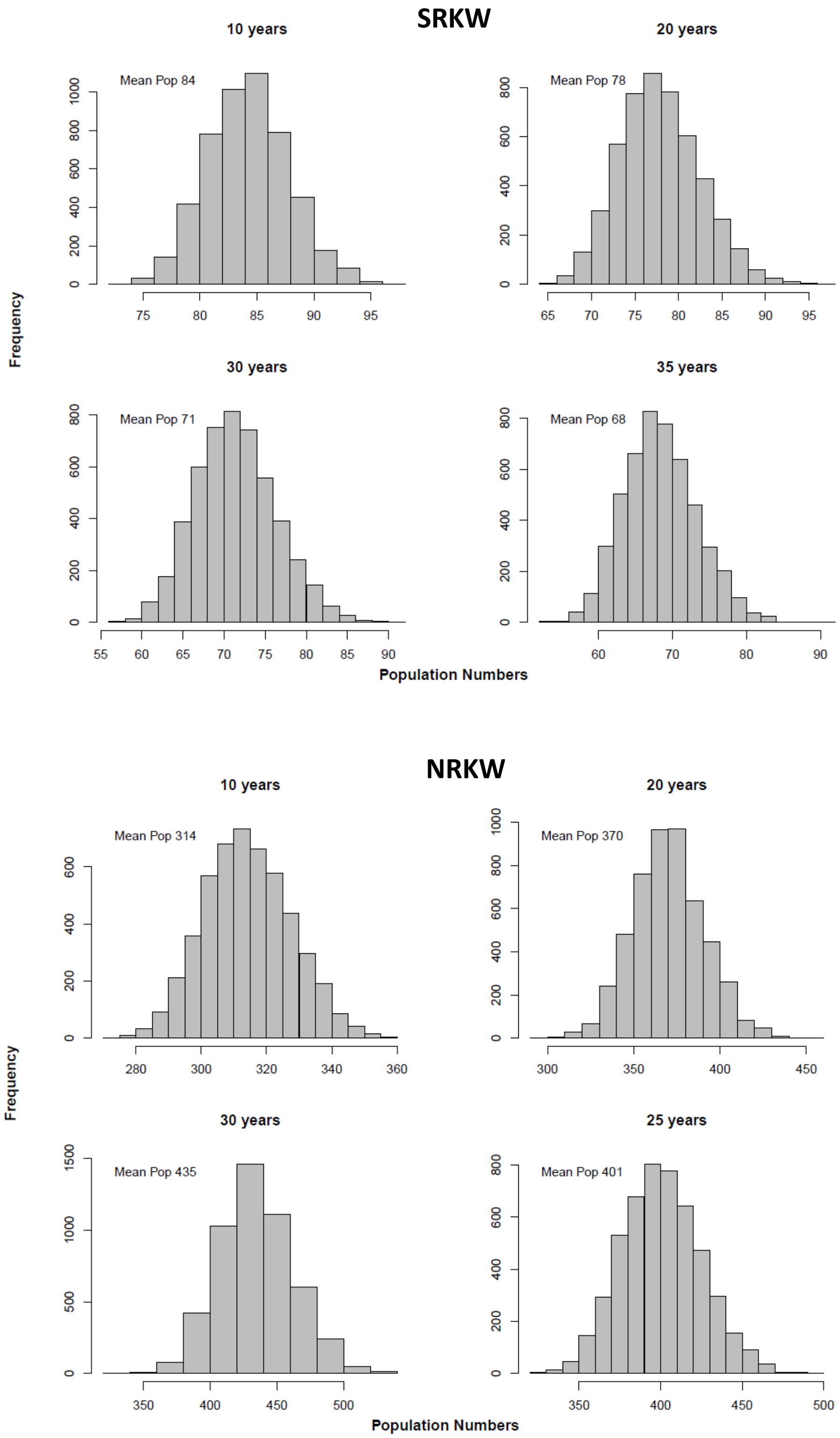


Figure 10. Projections of SRKW and NRKW population size under status quo conditions at 10, 20, 30, and τ years in the future (SRKW Damping Time τ = 35 years; NRKW Damping Time τ = 25 years). Histograms and computation of stochastic population growth generated from 5000 realizations of population size.

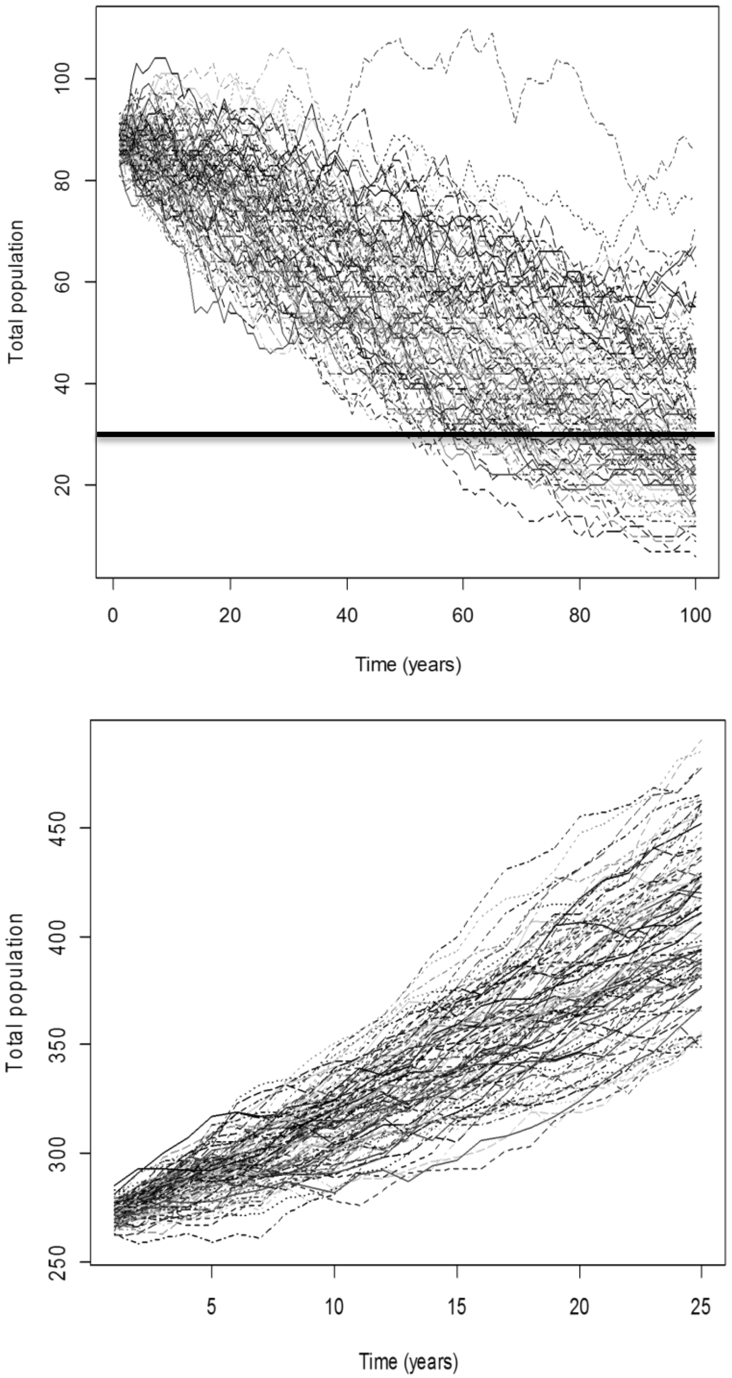


Figure 11. Projections (100) of SRKW (upper panel) and NRKW (lower panel) population size under demographic stochasticity and status quo conditions. Horizontal line for SRKW shows the 30-individual quasi-extinction threshold.

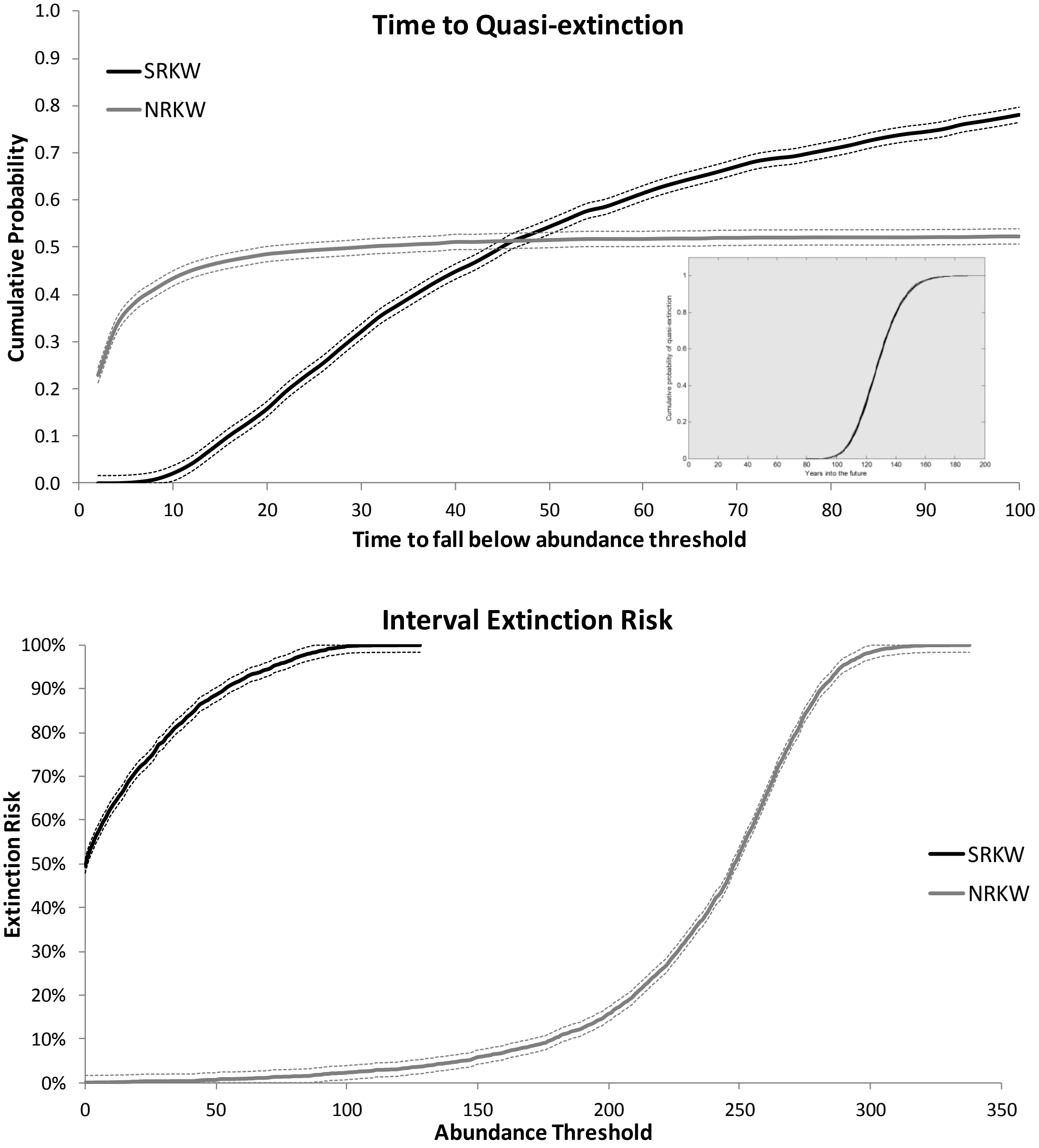


Figure 12. Time to quasi-extinction and interval extinction risk for SRKW and NRKW. ‘Time to quasi-extinction’ shows the probability of population falling below abundance thresholds of 30 for SRKW and 250 for NRKW in the future (yr) under environmental and demographic stochasticity and status quo conditions. Inserted in the upper panel, and for comparison, is the probability of SRKW’s population size falling below 30 individuals in the future in an IID environment. ‘Interval extinction risk’ shows the probability of population size falling below a population threshold in 100 years under environmental and demographic stochasticity and status quo conditions. Both figures show mean and 95% CIs generated from 10,000 replications.

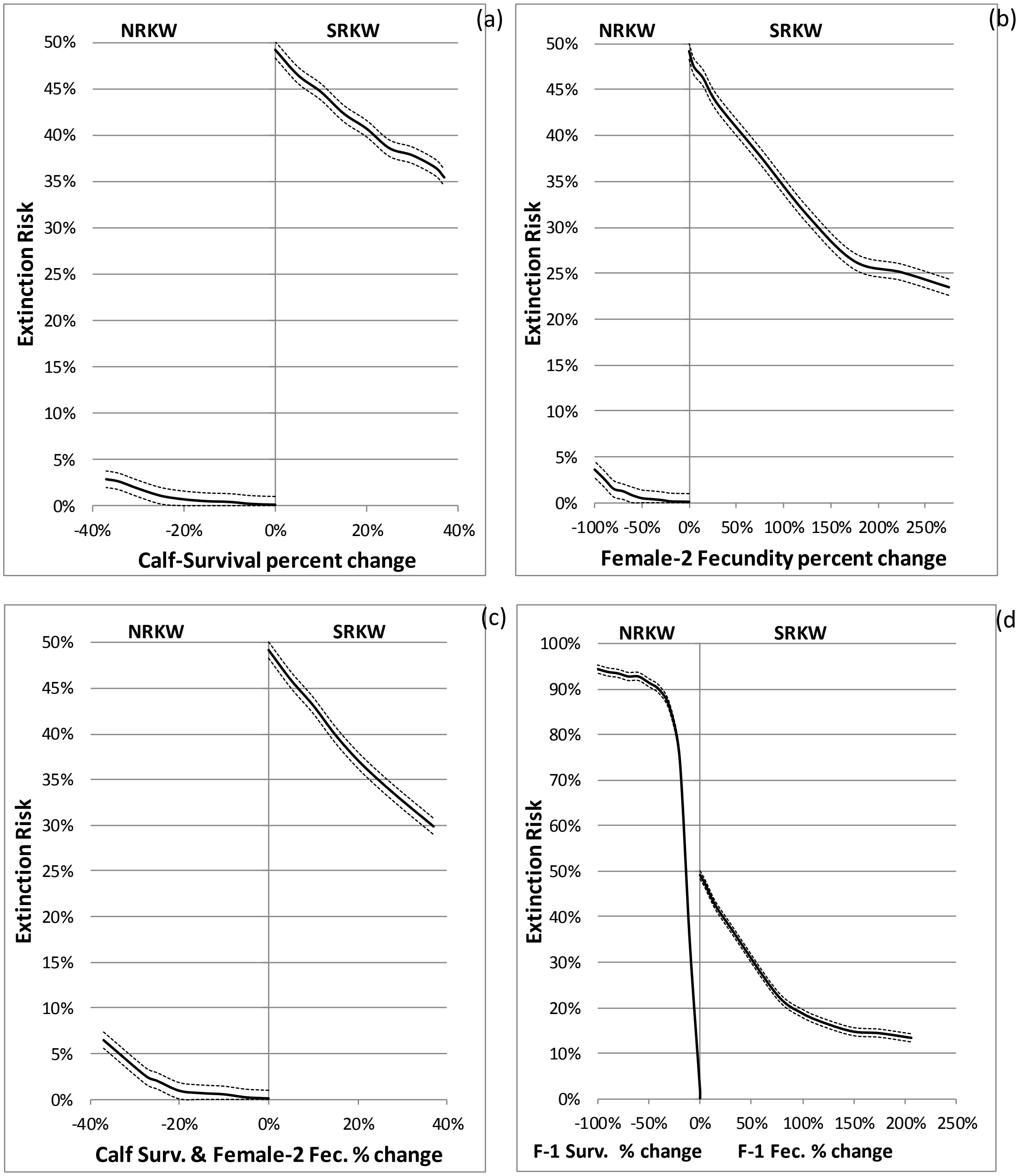
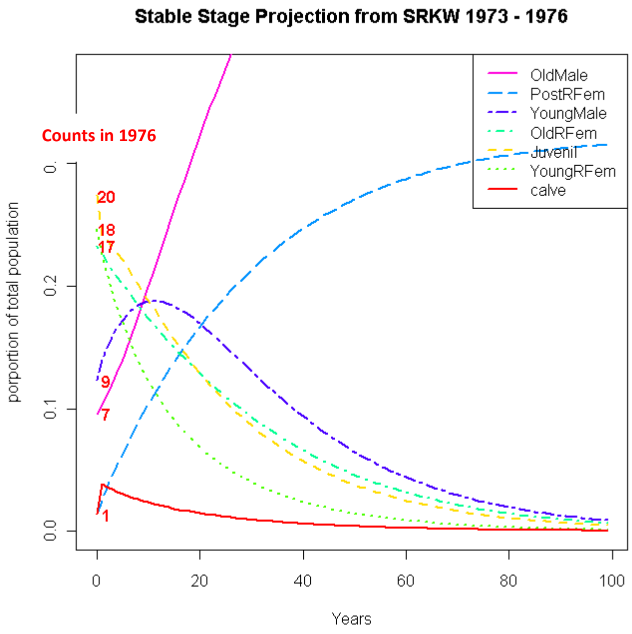


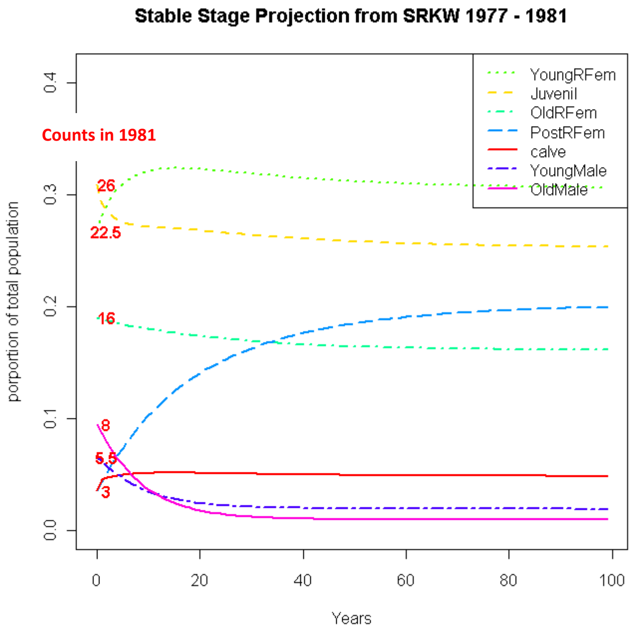
Figure 13. Extinction risk in 100 years in response to positive perturbations to selected vital rates in SRKW and negative perturbations to selected vital rates in NRKW. (a) Viable calf survival. (b) Fecundity of old reproductive females (Female-2). (c) Viable calf survival and Female-2 fecundity. (d) Fecundity of young reproductive females (F-1) in SRKW and survival of young reproductive females in NRKW.

9.0. APPENDICES

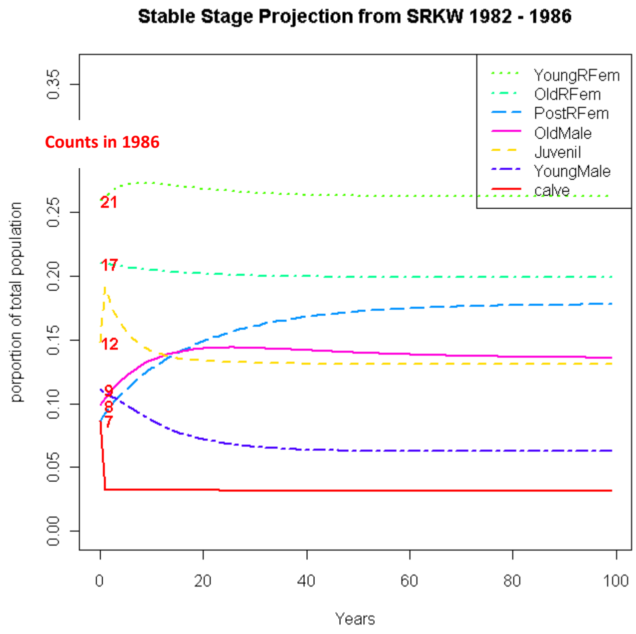
9.1. Appendix A. Projections of observed stage distributions towards stable stage distributions for SRKW and NRKW in the period between the end of the live-capture fishery and the first year used for the analyses in this report (1987). The projections represent the periods 1973-1976, 1977-1981, 1982-1986, and the entire period 1973-1986. Observed and stable stage distributions differ substantially from those in 1987-2011, particularly for SRKW. The live-capture fishery targeted mostly SRKW. Olesiuk et al. (1995) estimated 48 individuals (mostly juveniles and young males) were taken from the SRKW population between 1965 and 1973.



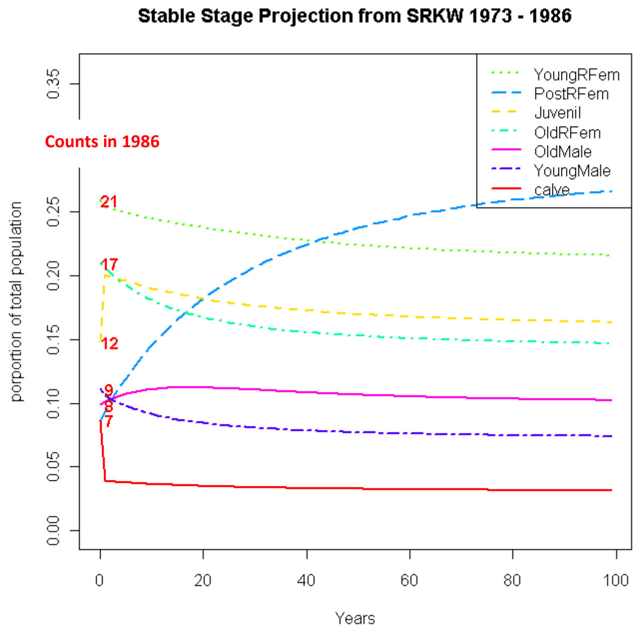
Stable Stage Projection from SRKW 1973 - 1976
OldMale
PostRFem
YoungMale
OldRFem
Juvenil
YoungRFem
calve
Counts in 1976
20
18
17
9
7
1
porportion of total population
0.0
0.1
0.2
0.
0
20
40
60
80
100
Years



Stable Stage Projection from SRKW 1977 - 1981
YoungRFem
Juvenil
OldRFem
PostRFem
calve
YoungMale
OldMale
Counts in 1981
26
22.5
16
8
5.5
3
porportion of total population
0.0
0.1
0.2
0.3
0.4
0
20
40
60
80
100
Years

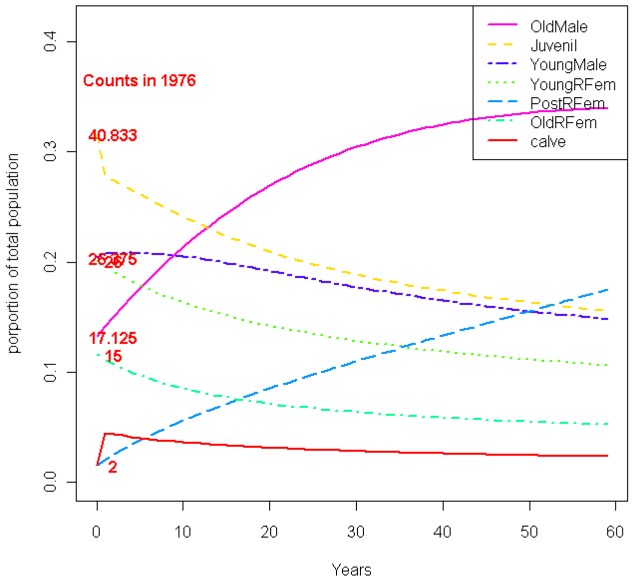


Stable Stage Projection from SRKW 1982 - 1986

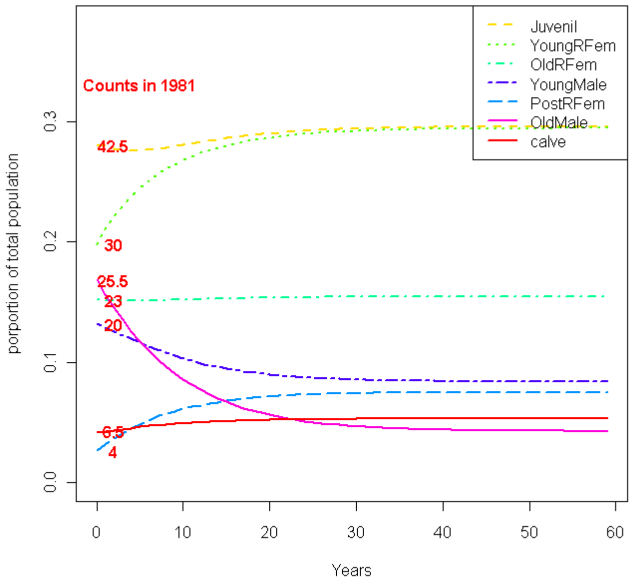


Stable Stage Projection from SRKW 1973 - 1986

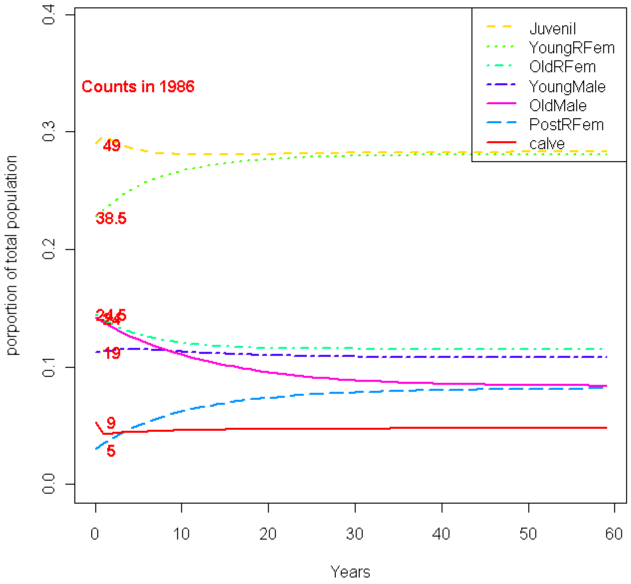
Stable Stage Projection from NRKW 1973 - 1976



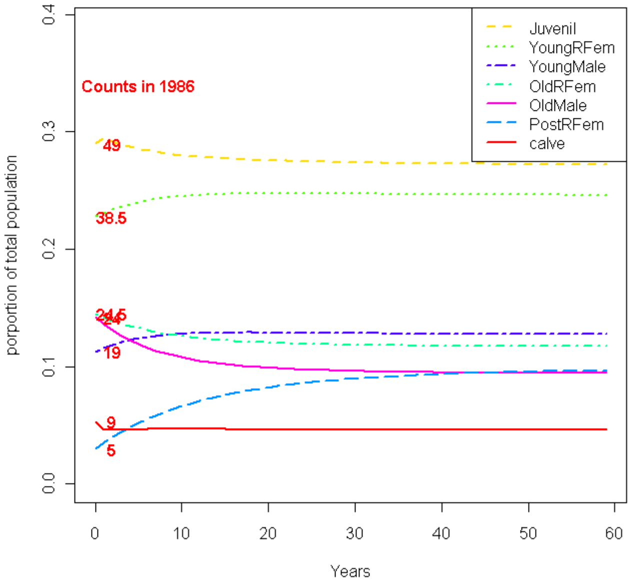
Stable Stage Projection from NRKW 1977 - 1981



Stable Stage Projection from NRKW 1982 - 1986



Stable Stage Projection from NRKW 1973 - 1986



9.2. Appendix B. Time series of vital rates and total population abundance for SRKW and NRKW (1987-2011). Female 1: young reproductive female; Female 2: old reproductive female; Female 3: post-reproductive female; Male 1: young mature male; Male 2: old mature male.

Year	Pop	Calf Surv.	Juvenile Surv.	Female 1 Surv.	Female 2 Surv.	Female 3 Surv.	Male 1 Surv.	Male 2 Surv.	Female 1 Fec.	Female 2 Fec.	Abundance
1987	SRKW	0.7500	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.1500	0.0571	84
1988	SRKW	0.0000	1.0000	1.0000	1.0000	1.0000	0.7619	1.0000	0.0952	0.0000	85
1989	SRKW	1.0000	1.0000	1.0000	1.0000	0.8571	1.0000	1.0000	0.0500	0.0556	83
1990	SRKW	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.2500	0.0000	87
1991	SRKW	0.7500	0.9444	1.0000	1.0000	1.0000	1.0000	0.9500	0.1000	0.1081	91
1992	SRKW	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.1111	0.0500	91
1993	SRKW	0.8333	0.9510	0.8750	0.9524	1.0000	1.0000	1.0000	0.2222	0.0952	97
1994	SRKW	1.0000	1.0000	1.0000	1.0000	1.0000	0.8571	0.7727	0.1000	0.0000	94
1995	SRKW	1.0000	1.0000	1.0000	0.8750	1.0000	0.8333	0.9000	0.1818	0.1143	96
1996	SRKW	1.0000	1.0000	1.0000	0.9157	0.6250	1.0000	0.9000	0.1667	0.0667	97
1997	SRKW	NA	0.9438	1.0000	1.0000	1.0000	1.0000	0.7500	0.0000	0.0000	91
1998	SRKW	1.0000	0.9405	0.9000	0.9537	1.0000	1.0000	0.6667	0.0833	0.0000	89
1999	SRKW	0.3333	1.0000	0.9550	0.8083	1.0000	1.0000	0.9286	0.1200	0.0000	85
2000	SRKW	0.6667	1.0000	1.0000	0.8571	1.0000	0.9000	0.5714	0.1200	0.0000	82
2001	SRKW	0.6667	1.0000	0.9750	1.0000	1.0000	1.0000	1.0000	0.1702	0.0000	80
2002	SRKW	1.0000	1.0000	1.0000	1.0000	0.8000	1.0000	0.8000	0.0000	0.0800	80
2003	SRKW	0.8333	1.0000	1.0000	1.0000	0.7778	1.0000	1.0000	0.2273	0.0769	84
2004	SRKW	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	0.0435	0.0769	84
2005	SRKW	0.7143	0.7857	1.0000	1.0000	0.8750	1.0000	1.0000	0.1667	0.3077	91
2006	SRKW	0.3333	1.0000	0.9545	0.9375	1.0000	0.9688	1.0000	0.1250	0.0000	89
2007	SRKW	1.0000	0.9714	1.0000	1.0000	0.7500	1.0000	1.0000	0.0526	0.1250	87
2008	SRKW	0.3333	1.0000	0.9697	0.9750	0.8333	1.0000	1.0000	0.0000	0.1250	88
2009	SRKW	1.0000	1.0000	1.0000	0.9375	0.9167	1.0000	0.6667	0.0556	0.1290	87
2010	SRKW	0.8333	1.0000	1.0000	1.0000	0.8333	0.9286	0.6000	0.2632	0.2000	88
2011	SRKW	NA	NA	NA	NA	NA	NA	NA	0.0526	0.0667	88
1987	NRKW	1.0000	0.9931	1.0000	0.9702	0.7857	1.0000	1.0000	0.2368	0.0833	177
1988	NRKW	0.8571	0.9926	1.0000	0.8821	0.8750	1.0000	1.0000	0.1647	0.0000	182
1989	NRKW	1.0000	0.9990	1.0000	1.0000	1.0000	1.0000	0.9744	0.0870	0.1277	185
1990	NRKW	1.0000	0.9875	1.0000	0.9484	0.8571	0.9484	0.8974	0.1489	0.1200	194
1991	NRKW	0.9833	0.9899	0.9917	0.9872	0.9524	1.0000	1.0000	0.1443	0.1333	197
1992	NRKW	1.0000	0.9410	0.9900	1.0000	0.9125	0.9444	0.9099	0.1176	0.0909	203
1993	NRKW	0.9500	0.9726	1.0000	0.9904	0.6238	1.0000	0.9589	0.0926	0.0000	200
1994	NRKW	1.0000	0.9609	1.0000	0.9694	0.9673	1.0000	0.9952	0.1622	0.1481	207
1995	NRKW	0.8571	0.9721	1.0000	0.9881	0.8242	1.0000	0.9853	0.0877	0.1000	210
1996	NRKW	0.8750	0.9694	0.9664	0.9857	0.7148	0.9991	0.9144	0.1152	0.0494	213
1997	NRKW	0.8462	0.9708	0.9895	0.9852	0.9391	0.9990	0.8087	0.2062	0.0476	218
1998	NRKW	1.0000	0.9417	0.9893	0.9775	0.8738	0.9330	0.8000	0.1203	0.0513	215
1999	NRKW	1.0000	0.9830	0.9707	0.9793	0.6896	0.9796	0.7731	0.1131	0.1714	215
2000	NRKW	0.6667	0.9223	0.9700	0.9667	0.8750	0.9417	0.8196	0.0775	0.0588	209
2001	NRKW	0.8750	0.9694	0.9867	1.0000	1.0000	0.9890	0.9375	0.1156	0.0500	201
2002	NRKW	0.9000	0.9709	1.0000	1.0000	1.0000	0.9444	0.9412	0.1186	0.1364	204
2003	NRKW	1.0000	0.9946	1.0000	1.0000	0.9375	1.0000	1.0000	0.0781	0.1333	205
2004	NRKW	0.9714	0.9854	1.0000	0.9861	0.8750	1.0000	1.0000	0.2015	0.2143	222
2005	NRKW	0.8750	0.9441	0.9690	0.9815	0.7500	0.9977	0.9211	0.1976	0.1250	236
2006	NRKW	0.9333	0.9740	0.9835	1.0000	1.0000	0.9429	0.9825	0.2180	0.0984	240
2007	NRKW	0.8462	0.9842	0.9728	1.0000	1.0000	0.9167	0.9750	0.1686	0.1000	246
2008	NRKW	0.7647	0.9969	0.9932	0.9889	0.7500	0.9697	0.8254	0.1770	0.1613	256
2009	NRKW	1.0000	0.9783	0.9926	1.0000	1.0000	0.9621	0.7895	0.1443	0.1250	258
2010	NRKW	0.9231	0.9767	0.9709	0.9967	1.0000	0.9818	0.9792	0.1505	0.1135	264
2011	NRKW	NA	NA	NA	NA	NA	NA	NA	0.1139	0.0811	268

Figure B1. Box plot of observed vital rates for SRKW (dark grey) and NRKW (light grey) corresponding to 1987-2011. The horizontal line shows the median. The bottom and top of the box show the 25th and 75th percentiles, respectively. The vertical dashed lines show 1.5 times the interquartile range of the data (~ 2 standard deviations). Points more than 1.5 times the interquartile range above the third quartile and points more than 1.5 times the interquartile range below the first quartile are plotted individually. Juv: Juvenile; F1: young reproductive female; F2: old reproductive female; F3: post-reproductive female; M1: young male; M2: old male.

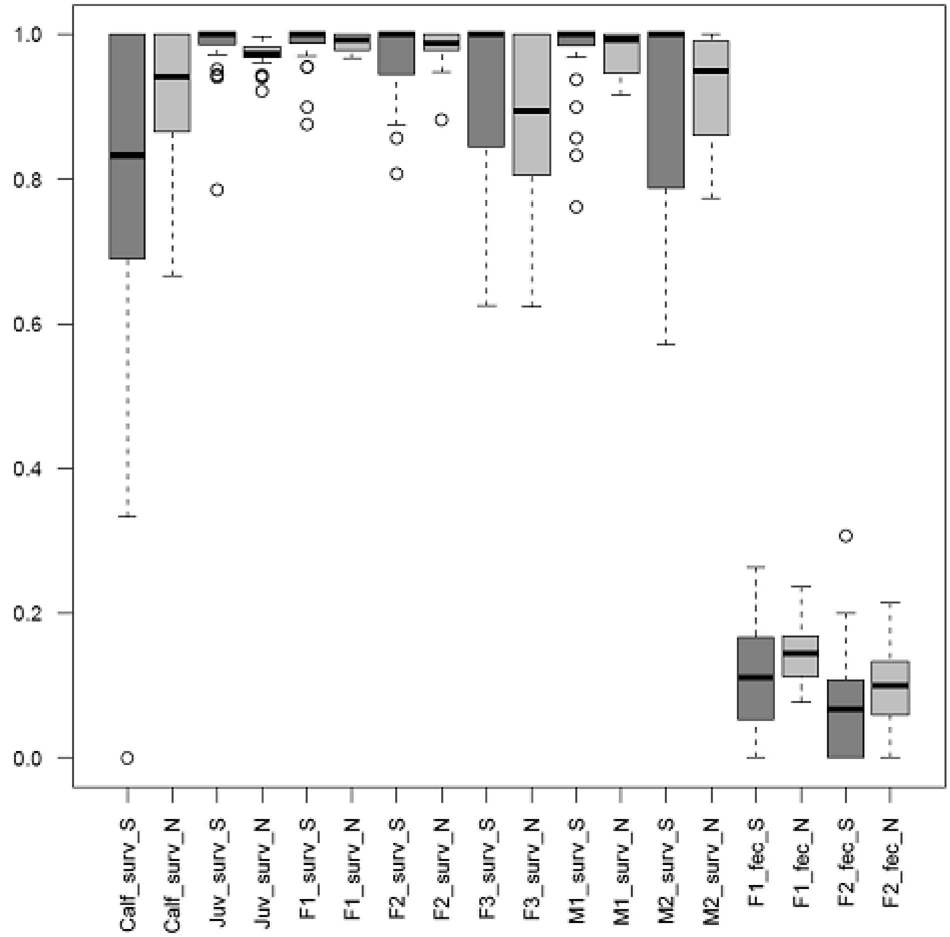
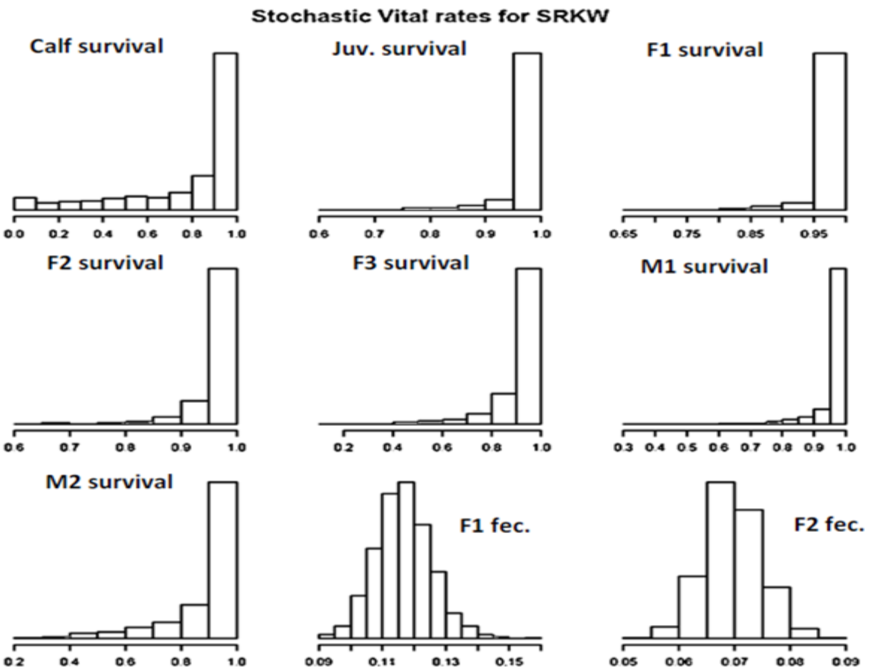
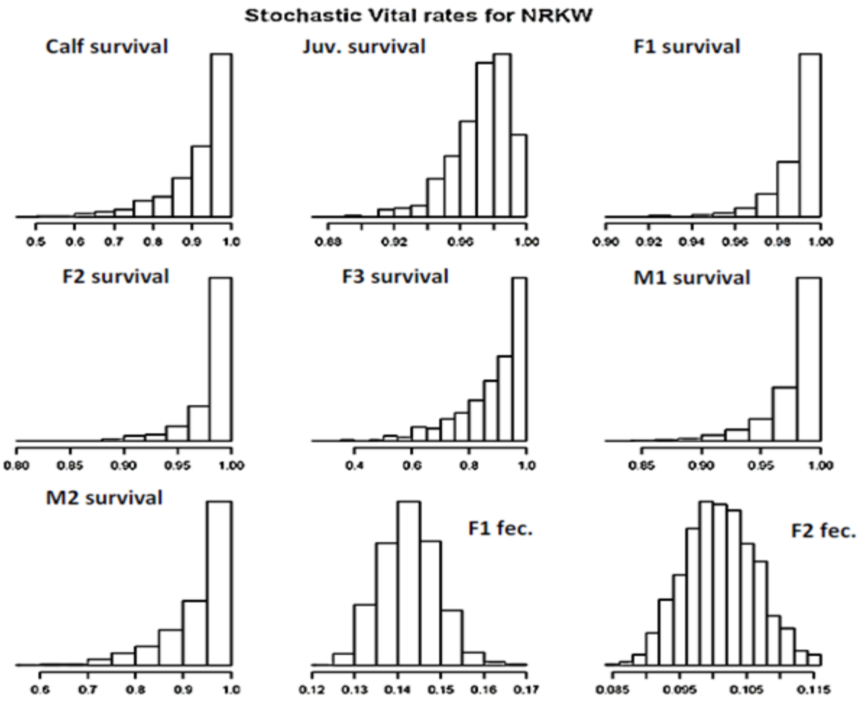


Figure B2. Histograms of stochastic vital rates generated from simulations (5000 replications) for SRKW and NRKW. The beta distribution was used for survival and the lognormal for fecundity. Juv: Juvenile; F1: young reproductive female; F2: old reproductive female; F3: post-reproductive female; M1: young male; M2: old male. Distributions were parameterized with means and variances of vital rates for the period 1987-2011.





9.3. Appendix C. Additional detail on analytical procedures used in this investigation

Life expectancy: The transition matrix **T**, which is a variant of matrix **M** with zeros in the fertility elements, was used to generate the fundamental matrix **N** = (**I** – **T**)-1, where **I** is a 7 x 7 identity matrix (with ones in the diagonal and zeros elsewhere). Matrix **N** gives the expected number of years spent in each stage before death, and life expectancies were computed as the column sums of **N** (Caswell and Fujiwara, 2004).

Retrospective analysis: Retrospective analyses were conducted with a population matrix sub-model including only those stages with contributions to λ. This sub-model (4 x 4 matrix) was therefore a truncated female-only model that excluded post-reproductive females, with $G_2 = \sigma_2 \gamma_2$, and μ_i as the product of mean offspring production by females in stage i and the proportion of females (φ_f).

Damping ratio: We also investigated the short-term or transient dynamics that dictate the rate of convergence to the stable stage distribution (SSD). This rate is governed by the second largest eigenvalue ($\lambda 2$; Lefkovitch, 1971), and a measure of the rate of convergence to the stable structure is the damping ratio $\rho = \lambda / |\lambda_2|$ where convergence to the SSD depends on how close ρ is to 1. The damping time is defined as $\tau = \ln(z)/\ln(\rho)$ (Haridas and Tuljapurkar, 2007), where z is the number of times the contribution of λ becomes as great as that of λ_2. Damping times at $z = 10$ were used to define minimum time horizons for projections of population size.

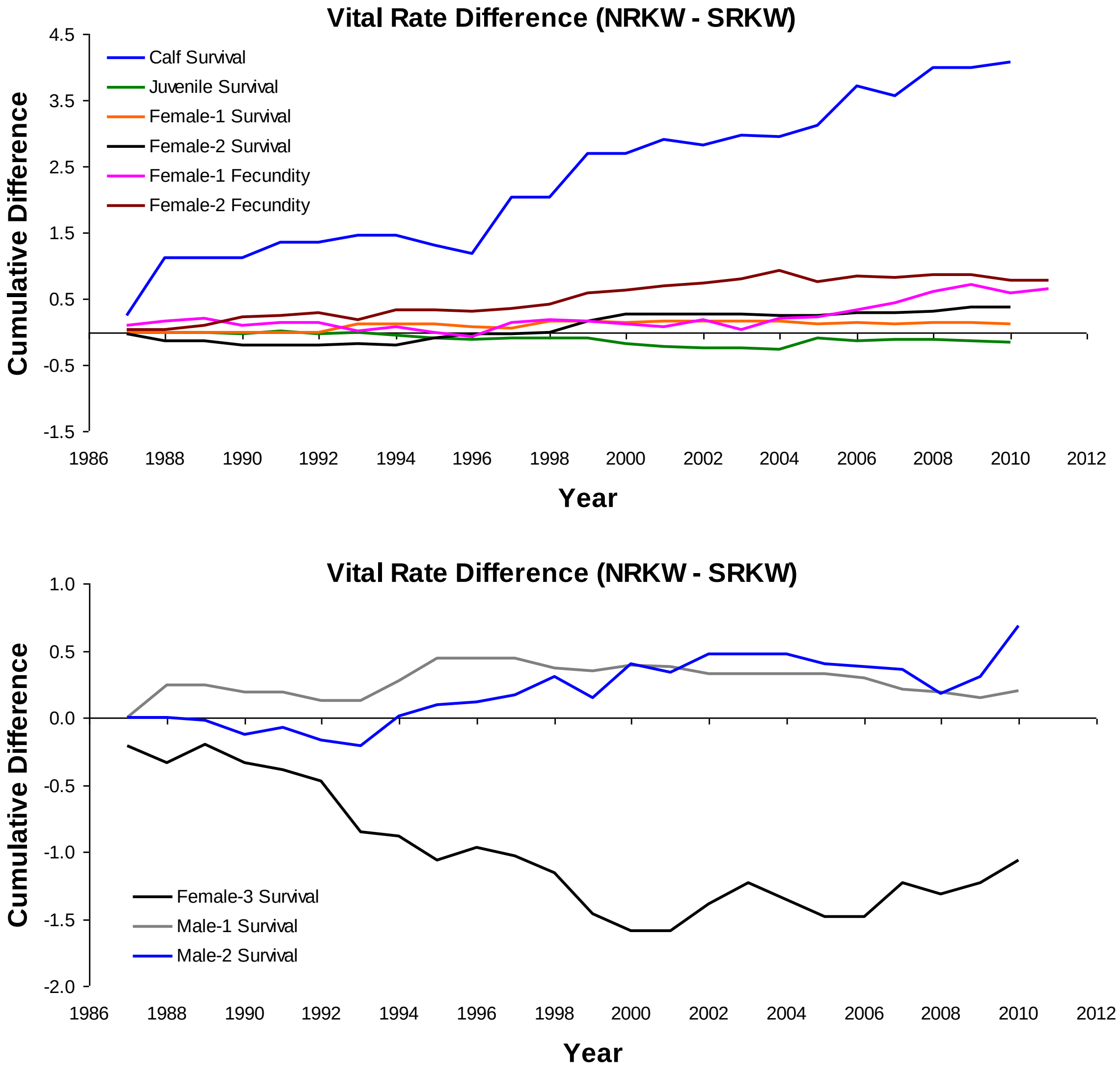
Demographic stochasticity: which is the temporal variation in population growth driven by chance variation in the actual fates of different individuals within a year, was modeled by sampling the number of survivors from a binomial distribution with parameters P_i and $N_i(t)$ as sample size and the number of calves from a Poisson distribution with mean $F_i \cdot N_i(t)$. Fecundity and survival rates were correlated within each modeled population to maintain their covariation structure and survival rates were constrained to values between 0 and 1, with the sum of all survival transitions from a given stage being ≤ 1 in any time step (see Akcakaya, 2002).

Caswell, H., and Fujiwara, M. 2004. Beyond survival estimation: mark-recapture, matrix population models, and population dynamics. Animal Biodiversity and Conservation 27, 471-488.

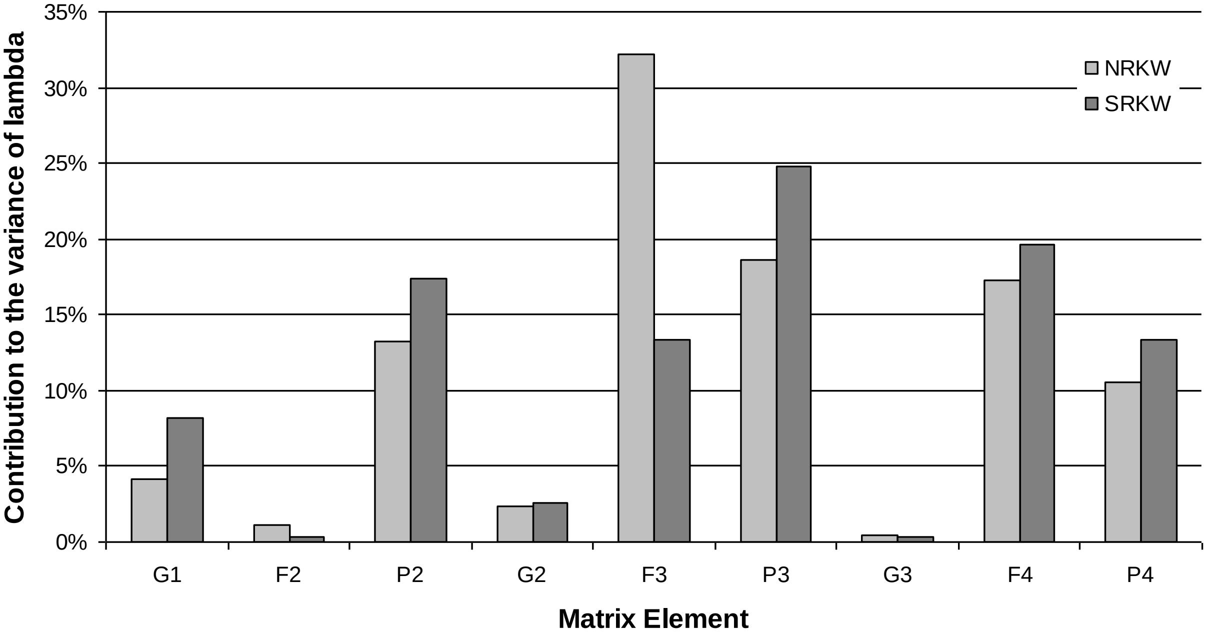
Haridas, C.V., and Tuljapurkar, S., 2007. Time, transients and elasticity. Ecol. Lett. 10: 1143-1153.

Lefkovitch, L.P. 1971. Some comments on the invariants of population growth, in: Patil, G.P., Pielou, E.C., Walters, W.E. (Eds.). Statistical Ecology, Volume 2. Pennsylvania State University Press, Pennsylvania, pp. 337-360.

9.4. Appendix D. Cumulative difference between vital rates of NRKW and SRKW for years 1987-2011. The top panel shows the cumulative difference for vital rates contributing directly to population growth and the bottom panel for vital rates not contributing directly to population growth.



<u>9.5. Appendix E.</u> Contributions of matrix elements to the variance in population growth for 1987-2011. See Figure 2 and Equation 2 in main manuscript for definitions of matrix elements.



9.6. Appendix F. Realized population growth.

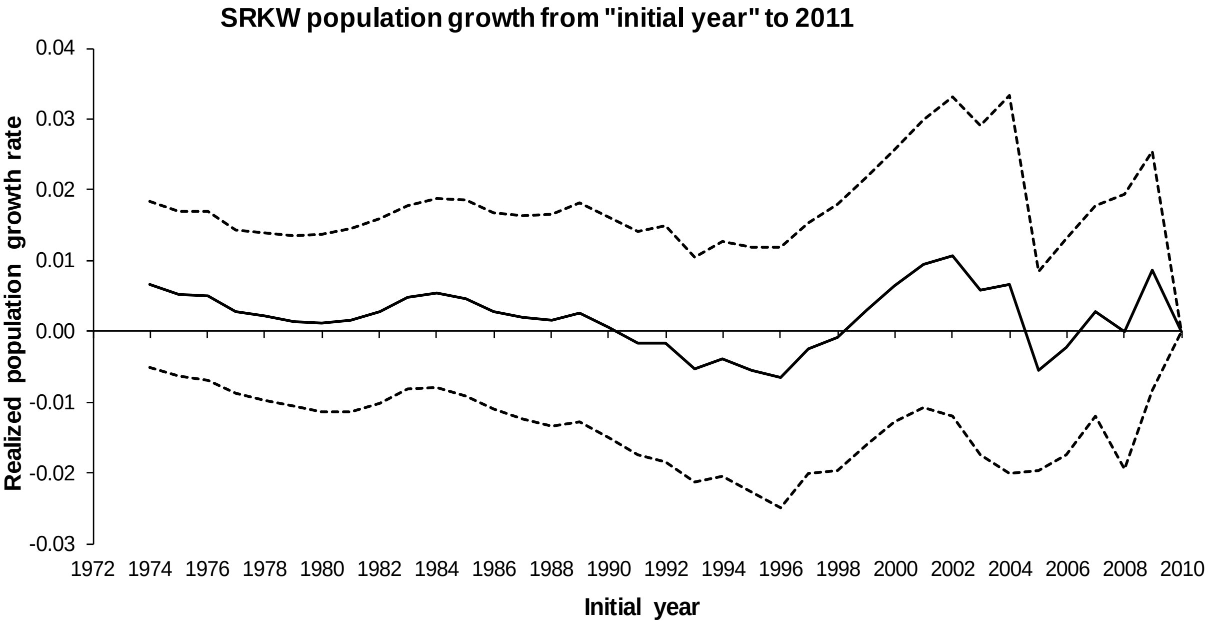
The population growth rate derived from a demographic projection matrix (λ) represents the expected population growth rate under asymptotic dynamics (assuming vital rates means and variances are going to remain stable in the long term) and not the realized population growth (*r*), which is the observed rate of change computed from counts of total population size. To illustrate these differences for both killer whale populations, and to evaluate their past population dynamics, realized population growth for a given annual interval was computed as $r_t = \ln(N_{t+1}/N_t)$ and the long-term realized population growth rate ($r_{a\to z}$) as:

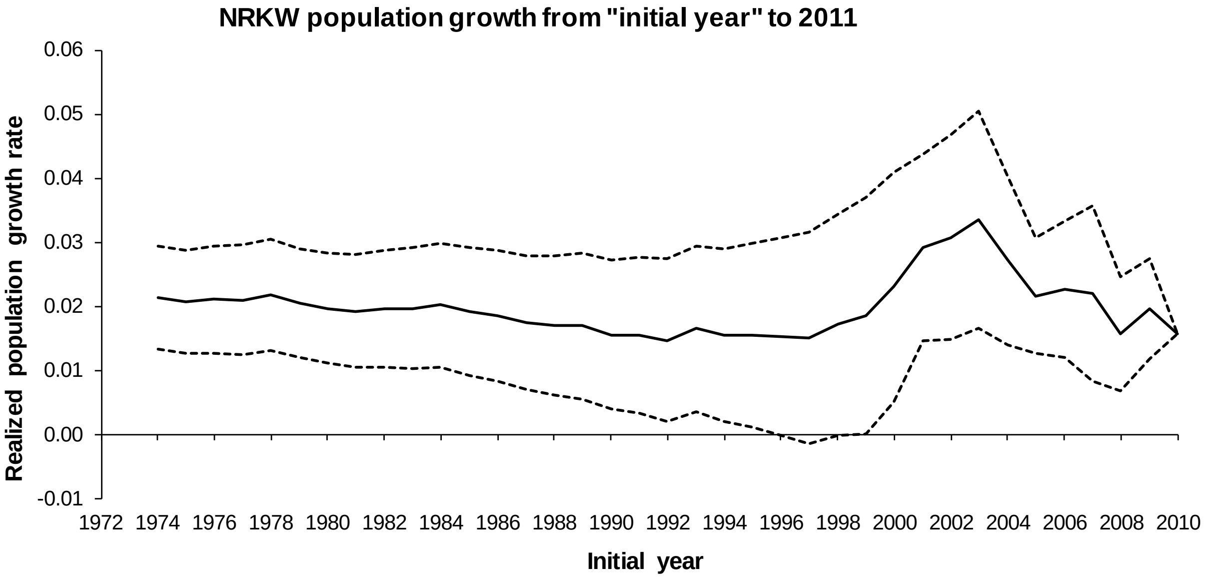
$$r_{a\to z} = \frac{\sum_{t=a}^{y} \ln\left(N_{t+1}/N_t\right)}{z-a}$$

where *a* and *z* represent the first and last years of the time series, respectively, and $y = z - 1$. The phenology of realized population growth across the entire time series (1974-2011) was generated by computing $r_{a\to z}$ with z = 2011 and annual steps of *a* progressing from 1974 to 2010. These phenologies referenced to year 2011 show also the sensitivity of estimated long-term realized population growth to the extent of the time series. Unlike this section, the following sections will make reference to λ, the demographic parameter representing the expected population growth.

Annual rates of change, based on population counts during 1974-2011, ranged from -6.4% to 8.0% in SRKW and from -3.9% to 7.8% in NRKW with mean rates of change of 0.6% for SRKW and 2.0% for NRKW. In spite of annual rates of change of the two populations being poorly correlated (r = 0.33), their phenologies of long-term realized population growth referenced to year 2011 (Figure F.1) were moderately correlated (r = 0.67), thus showing greater covariation for long-term realized population growth than for annual intervals. The lower 95% confidence limit for SRKW's phenology was consistently negative during 1974-2011 and as low as -2.5% whereas for NRKW it was positive in all years excepting for time series starting in 1996-1999 with a minimum of -0.16% for initial year 1997. Long-term realized population growth was more sensitive to the extent of the time series for SRKW than for NRKW. Mean realized population growth of SRKW declined consistently, reaching negative values, as the initial year moved from 1974 to 1996. Both phenologies showed an increase in realized population growth from 1998 to 2002 (2003 in NRKW) and a general decline afterwards. The larger variation in the realized population growth of SRKW and NRKW in the final years of the time period is a function of both actual inter-annual variation in population size and the shrinkage of the time series as initial year approaches year 2011.

Figure F.1. Phenology of realized population growth rate (1974-2011) with annual steps progressing from 1974 to 2010 for SRKW and NRKW. Mean (solid lines) and 95% C.I. (dashed lines) are shown.





This is the end of this report.

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