

Relative importance of chinook salmon abundance on resident killer whale population growth and viability

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ABSTRACT

1. Two distinct populations of resident killer whales (*Orcinus orca*) in the north-eastern Pacific Ocean have been listed in Canada and the USA as being of conservation concern. One of the major threats recognized for these two populations is nutritional stress associated with prey abundance levels and availability.

2. The predominance of chinook salmon (*Oncorhynchus tshawytscha*) in the summer diets of both killer whale populations has been shown by recent studies, and correlations between indices of chinook salmon abundance and resident killer whale (RKW) vital rates have generated hypotheses about the potential for chinook salmon abundance to limit RKW population dynamics.

3. This study merges statistical inference derived from linkages between RKW vital rates (survival probability and fecundity rates) and chinook salmon abundance with demographic perturbation analysis and population viability analysis to address some of the pressing questions that have recently engaged the efforts of scientists and managers interested in: (1) the role of chinook salmon abundance in the population dynamics of RKW; and (2) how RKW population viability is expected to respond to changes in chinook mortality owing to harvest.

4. Numerous interactions between the abundance of chinook salmon aggregates and RKW vital rates were found and deemed to result from predator–prey dynamics. However, the results of this present analysis also indicated that the effects of these interactions on RKW population growth and viability are relatively small and/or uncertain and in need of further research.

5. Other factors (genetic, environmental and/or anthropogenic) could be at play limiting RKW population growth and possibly masking and confounding the detection of stronger interactions between RKW vital rates and chinook salmon abundance. Given the current state of information, it is highly uncertain whether the allocation of chinook salmon resources for RKW would be an effective management action in RKW recovery plans.

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INTRODUCTION

Two distinct populations of resident killer whales (*Orcinus orca*) in the north-eastern Pacific Ocean have been listed in Canada and the USA as being of conservation concern. The southern resident killer whale (SRKW) population is currently listed as endangered in both countries under the Species At Risk Act and the Endangered Species Act (COSEWIC, 2008; NMFS, 2008) whereas the northern resident killer whale (NRKW) population has been listed as threatened in Canada under the Species At Risk Act (COSEWIC, 2008). The major threats recognized for these two populations are nutritional stress associated with prey abundance levels and availability, pollution and contaminants, and disturbances from vessels and sound (COSEWIC, 2008; NMFS, 2008). In spite of their home range overlap (Figure 1) 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 whereas NRKW population size has been generally increasing for the last four decades with 268 individuals at the end of 2011 (Vélez-Espino *et al.*, 2014).

The predominance of chinook salmon (*Oncorhynchus tshawytscha*) in the summer diets of both killer whale populations has been shown by recent studies, and the availability of this species of Pacific salmon has been identified as a potential limiting factor to the population dynamics of both SRKW and NRKW (COSEWIC, 2008; Ford *et al.*, 2010a, b). Field studies have also demonstrated strong resident killer whale selectivity for chinook salmon even when chinook abundance was low relative to other salmonids (Ford and Ellis, 2006). Chinook salmon eaten by these two killer whale populations in their late spring–early autumn ranges and critical habitats¹ (Figure 1) originate mainly from Fraser River and Puget Sound populations in the case of SRKW (Hanson *et al.*, 2010) and Fraser

River populations in the case of NRKW (Ford and Ellis, 2006; Ford *et al.*, 2010a). Chinook salmon from Northern British Columbia (BC), Central BC, West Coast Vancouver Island (WCVI), Georgia Strait, Puget Sound, and Upper Columbia River have also been identified as important in the late spring–early autumn diet of NRKW (Ford and Ellis, 2006; Ford *et al.*, 2010a). Some of the salmon stocks consumed by resident killer whales are part of the Puget Sound chinook salmon Evolutionarily Significant Unit listed as threatened in the USA². In addition, the North Puget Sound spring-run and autumn-run chinook salmon stocks and several Fraser River spring-run and summer-run stocks have been identified as having medium to high conservation concern in the strategic plan of the Pacific Salmon Commission's Southern Fund Committee.³ Diet composition outside of the late spring–early autumn ranges is poorly known in comparison, but data from predation events sampled during winter and early spring (Ford, 2012) seem to indicate a prevalence of chinook salmon in the year-round diet of both resident killer whale populations (RKW; hereafter used to refer to both SRKW and NRKW).

Extensive work has been conducted compiling and structuring life-history data for RKW (Bigg *et al.*, 1990; Olesiuk *et al.*, 1990; NWFSC, 2008; The Center for Whale Research, 2012), identifying prey in general (Ford *et al.*, 1998; Ford and Ellis, 2006) and the chinook salmon stocks predominant in the diet of RKW (Ford *et al.*, 2010a; Hanson *et al.*, 2010) as well as posing hypotheses on the role chinook salmon abundance plays in limiting RKW population dynamics (Ward *et al.*, 2009; Ford *et al.*, 2010b) and understanding the demography and population dynamics of these two populations (Olesiuk *et al.*, 1990; Brault and Caswell, 1993; Krahn *et al.*, 2002, 2004; Olesiuk *et al.*, 2005; Vélez-Espino *et al.*, 2014). Additional effort is now required to quantify RKW–chinook salmon interactions and their influence on RKW population growth rates and viability.

¹Critical habitats are situated on important migratory corridors for chinook salmon. Seasonal occurrence of RKW in these habitats is strongly associated with salmon abundance and foraging is the primary activity undertaken there. Other important life processes undertaken in these areas include resting, socializing, and mating (Ford, 2006). Critical habitats shown in Figure 1 have been officially designated under Canada's Species At Risk Act.

²<http://ecos.fws.gov/speciesProfile/profile/speciesProfile.action?spcode=E06D>

³http://fund.psc.org/2014/5_SF_2008_Strategic_Plan.pdf

KILLER WHALE-CHINOOK SALMON INTERACTIONS

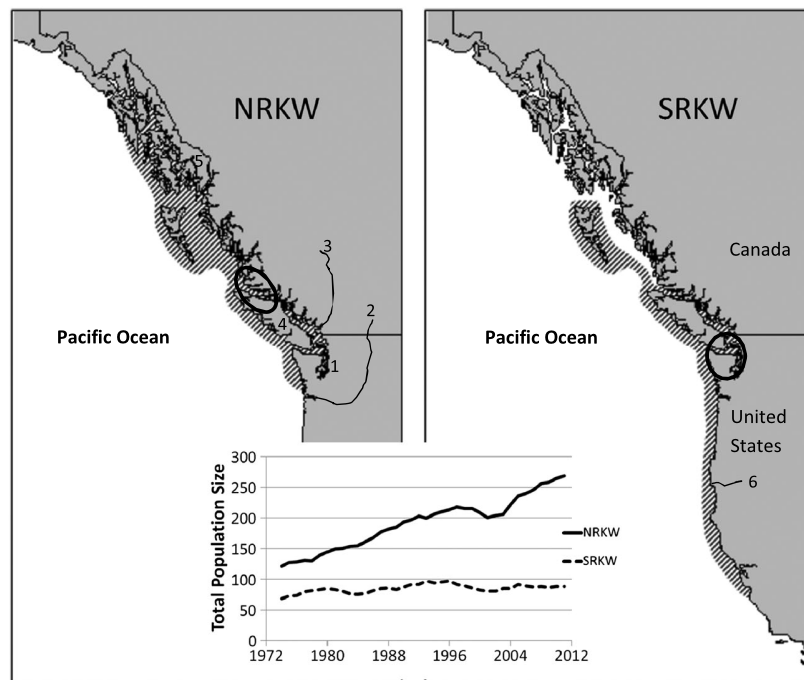


Figure 1. Known geographical ranges along the north-east Pacific Ocean and population trends of northern (left) and southern (right) resident killer whales. Circles show the critical habitats recognized for these two populations. 1: Puget Sound; 2: Columbia River; 3: Fraser River; 4: Vancouver Island; 5: South-east Alaska; 6: Klamath River.

This study merges statistical inference derived from linkages between killer whale vital rates (i.e. sex- and stage-specific survival probability and fecundity rates) and chinook salmon abundance with demographic perturbation analysis to address some of the pressing questions that have recently engaged the efforts of scientists and managers interested in: (1) the role of chinook salmon abundance on the population dynamics of endangered SRKW and threatened NRKW; and (2) how killer whale population viability is expected to respond to changes in chinook mortality owing to harvest. These objectives were addressed through perturbation analyses of stochastic matrix population models based on up-to-date demographic data and constructed to represent resident killer whale population dynamics in detail while facilitating the incorporation of vital rates as random variables or as functions of chinook abundance from individual stocks or stock aggregates. Perturbation analyses within the context of chinook salmon linkages are a novel contribution to our understanding of SRKW and NRKW

population dynamics that could inform future conservation and management decisions. In addition, a hypothesis framework is provided for the interpretation of linkages between killer whale demographic rates and chinook stock aggregates exhibiting different degrees of evidence from diet-composition studies.

MATERIALS AND METHODS

RWK data and demographic models

Demographic data for resident killer whales were obtained from 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 individual whales from natural markings. Surveys have occurred annually without interruption since 1973 for NRKW and since 1974 for SRKW. Each year, all observed

animals in the populations are photo-identified to establish the status of individuals (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. Although survey data go back to the early 1970s, this study focused on RKW demographic rates based on 1987–2011 data. This time period represents a RKW generation and includes high quality data with ~75% of the individuals in each population alive in 2011 born during the selected time period (Vélez-Espino *et al.*, 2014). This step was considered important because this time series includes mostly census data generated by direct observations (as opposed to reconstructed data; Olesiuk *et al.*, 1990) and removed from the analyses the effect on stage structures caused by the large live-capture RKW fisheries in the 1960s and 1970s (Vélez-Espino *et al.*, 2014).

Demographic population models developed by Vélez-Espino *et al.* (2014) were used to represent separately the life cycle of SRKW and NRKW as a two-sex, stage-structured projection matrix with seven life stages: (1) calves (individuals in the first year of life); (2) juveniles (past 1 year but immature (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 years old and older); (6) young mature males (ages 10–21); and (7) old mature males (22 years old and older).⁴ Accordingly, the life cycle of RKW (Figure 2) includes matrix elements P_i as the probability of surviving and remaining in stage i , G_i as the probability of surviving and moving to the next stage, and F_i as the fertility rate of stage i . Vital rates σ_i (annual survival probability of an individual in stage i) and μ_i (mean offspring production by females in stage i , hereafter referred to as ‘fecundity’ to differentiate from the ‘fertility’ matrix element F_i) are lower-level

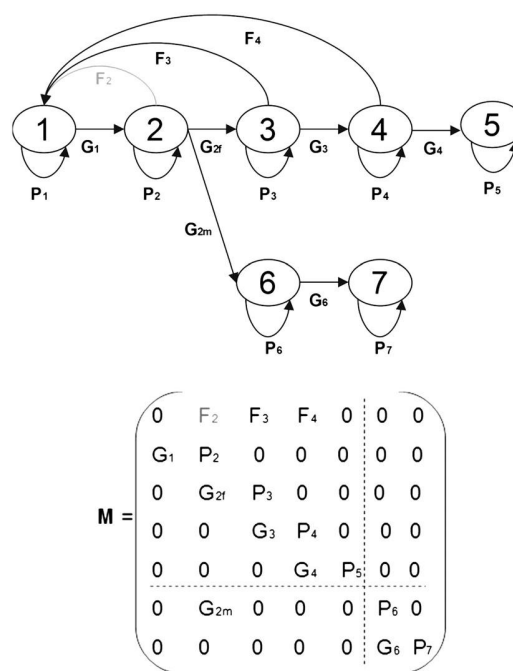


Figure 2. Stage-structured life cycle and corresponding projection matrix of resident killer whales with seven life stages: (1) calves; (2) juveniles; (3) young reproductive females; (4) old reproductive females; (5) post-reproductive females; (6) young mature males; and (7) old mature males. F_i represent 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 . The term F_2 represents the fertility of those juvenile individuals that mature during the projection interval.

parameters that form part of the computation of matrix elements as described in Vélez-Espino *et al.* (2014). A brief description of the matrix model is also available in Supplementary Material, Appendix S1. The dominant eigenvalue of population matrix M , corresponding to the stage-structured life cycle in Figure 2, is the expected population growth rate (λ) under asymptotic dynamics.

Chinook abundance and harvest data

Chinook stocks from northern California to south-east Alaska were included in these analyses, and two sources of chinook salmon abundance data were used. (1) Time series of vulnerable cohort abundance generated by the Pacific Salmon Commission's Chinook Model. These are the stock-specific estimated cohort abundances

⁴Note that, for practical reasons, some figures and tables use ‘Female 1’, ‘Female 2’, and ‘Female 3’ to refer to model stages 3, 4 and 5, and ‘Male 1’ and ‘Male 2’ to refer to model stages 6 and 7.

vulnerable to mixed stock ocean fisheries within the Pacific Salmon Treaty (PST) jurisdiction, which includes all chinook salmon stocks from north Oregon to south-east Alaska, including those stocks listed under the US Endangered Species Act. (2) Terminal run⁵ reconstruction indices (Kope and Parken, 2011) based on direct run reconstruction using coded wire tag recoveries for stocks from Canada, spring-runs in the Upper Columbia River, and stocks originating south of Cape Blanco, and using Pacific Salmon Commission's Chinook Model terminal run estimates for others (PSC, 2012).

Chinook salmon is an anadromous and semelparous species that spend 1–5 years in the ocean before returning to their natal streams to spawn (Groot and Margolis, 1991). For the exploration of fishing scenarios where changes in terminal run size occur as a result of changes in ocean (i.e. pre-terminal) harvest rates, terminal run equivalents (*TRE*) were used to account for the fact that only a portion of the fish not caught in ocean fisheries in a given year is expected to become part of the terminal run according to their maturation rates (*MR*), which are time variant and stock specific. Using up-to-date catch and *MR* data by age (*a*) from PSC exploitation rate analyses (PSC, 2012) for most stocks and from the Pacific Fishery Management Council (PFMC, 2012) for Sacramento Fall and Klamath Fall, *TRE* for an indicator stock⁶ by calendar year (*y*) were computed as:

$$TRE_{indicator,y} = \sum_{\text{PreTerm Fishery}} \sum_{a=3}^6 Catch_{a,y} * MR_{a,y} \quad (1)$$

Age-2 chinook were not included in Equation (1) because RKW prey mostly on age-3 and older chinook (Ford and Ellis, 2006). *TREs* were then

used to compute both proportional increases in terminal run size in the absence of pre-terminal (i.e. ocean) fishing and the terminal run scalars resulting from a specified change in ocean harvest rates in exploitation rate indicator stocks. These scalars were then used to calculate changes in terminal run of a stock of interest (more details in Supplementary Material, Appendix S2).

Evaluation of RKW–chinook interactions

Rarely is one line of evidence sufficient to demonstrate causation, and assembling information from various sources is useful to determine the weight-of-evidence (Burkhardt-Holm and Scheurer, 2007). Box 1 details two hypotheses for each RKW population, where hypotheses 1a for SRKW and 1b for NRKW correspond to RKW–chinook salmon interactions supported by evidence from diet-composition studies. Statistical significance in these interactions would provide stronger weight-of-evidence for causation than the remaining hypotheses 2a (SRKW) and 2b (NRKW). Statistical significance of hypotheses 2a or 2b would provide weaker weight-of-evidence for causation because they rest on the assumption that chinook salmon from specific stock aggregates are an important component in the diet of RKW from late autumn to early spring (or year-round) and outside their critical habitats.

The selection of stocks considered in hypotheses 2a and 2b were based on three criteria: stock size, and both temporal and spatial overlap with RKW. The probability of RKW encountering and preying on specific chinook stocks would directly depend on the size of the stock or stock aggregate (i.e. the larger the stock the greater the probability of encounter), its ocean distribution (juveniles of most chinook stocks disperse northwards along the coast, followed by a southward homing migration of maturing adults; Groot and Margolis, 1991), and its terminal-run timing and distribution. The final selection of stocks and stock aggregates to be considered under each hypothesis was determined using RKW and chinook salmon expert opinion, based on those criteria.

⁵Chinook salmon are anadromous fish that return (with high fidelity) to their natal streams when mature and after spending 1–5 years in the ocean. The terminal run comprises the mature fish that escape ocean fisheries and return to their natal streams to spawn and die.

⁶Indicator stocks are chinook salmon stocks whose exploitation rates are monitored through statistics derived from coded wire tagged fish recovered in fisheries and escapement.

Box 1. Hypotheses addressed in this investigation regarding RKW–chinook salmon interactions.

- Hypothesis 1a (based on diet composition studies):
There is a strong link between SRKW population growth and the terminal run size¹ of Fraser Early, Fraser Late, and Puget Sound Chinook stocks²
- Hypothesis 1b (based on diet composition studies):
There is a strong link between NRKW population growth and the terminal run size¹ of Northern British Columbia (BC), Central BC, West Coast Vancouver Island (WCVI), Upper Georgia Strait, and Lower Georgia Strait Chinook salmon stocks as well as the ocean (pre-terminal) abundance of Fraser Early, Puget Sound, and Upper Columbia Chinook stocks²
- Hypothesis 2a (assuming Chinook salmon remains an important diet component from late autumn through early spring and outside identified critical habitats):
There is a strong link between SRKW population growth and the terminal run size of large stocks such as Sacramento Fall, Klamath Fall, Columbia Upriver Brights, Columbia Spring/Summer/Fall, Oregon Coastal, WCVI, or coastwide (excluding Northern BC, Central BC, and South-east Alaska³), as well as the ocean (pre-terminal) abundance of ocean-type⁴ stocks with large contributions to ocean fisheries such as WCVI, Columbia Upriver Brights, Fraser Late, Oregon Coastal, Puget Sound, or coastwide (excluding South-east Alaska⁵)
- Hypothesis 2b (assuming Chinook salmon remains an important diet component from late autumn through early spring and outside identified critical habitats):
There is a strong link between NRKW population growth and the terminal run size of Fraser Early and Puget Sound⁶, and large stocks such as Columbia Upriver Brights, Columbia Spring/Summer/Fall, Fraser Late, Oregon Coastal, or coastwide (excluding Sacramento Fall, Klamath Fall⁷ but including South-east Alaska⁸), as well as the ocean (pre-terminal) abundance of ocean-type³ stocks with large contributions to ocean fisheries such as WCVI, Fraser Late, Oregon Coastal, or coastwide (excluding South-east Alaska⁵)

1 The terminal run includes terminal catch, which occurs mostly after fish are available for killer whales, and therefore represents the Chinook available for RKW in their late spring–early autumn ranges.

2 Based on diet composition studies.

3 Out of the known preferred geographic range of SRKW.

4 Ocean-type Chinook stocks spend most of their ocean life in coastal waters and are therefore within known RKW geographic range.

5 South-east Alaska Chinook salmon stocks perform extensive offshore oceanic migrations, and it is unlikely they are available for RKW. These stocks contribute on average less than 1% to the Chinook salmon available for PST ocean (pre-terminal) fisheries.

6 Although Fraser Early is not among the larger stocks, NRKW encounters with both Puget Sound and Fraser Early terminal runs could be greater than determined by previous observations (Riera, 2012).

7 Out of the known preferred geographic range of NRKW.

8 Within the known geographic range of NRKW.

NOTE: Chinook salmon stocks exhibiting autumn runs are identified as ‘Fall’ stocks (e.g. Sacramento Fall) in the Pacific salmon scientific and management arenas.

Associations between RKW vital rates (fecundity and survival) and chinook abundance were evaluated in light of the four hypotheses in Box 1 using beta regressions (Cribari-Neto and Zeileis, 2010). Beta regressions were used because they incorporate features such as heteroscedasticity or

skewness which are commonly observed in data taking values in the standard unit interval, such as rates or proportions. Abundance lags of 0-year and 1-year were used to examine relationships with survival rates whereas 0-year, 1-year, and 2-year abundance lags were used to examine

relationships with fecundity. The rationale for the use of lag-1 models for survival is that the effects of nutritional stress could be capitalized on mortalities the next year after food shortage occurred. The study of Ford *et al.* (2005) revealed that mortality indices were most highly correlated with changes in chinook abundance after a lag of 1 year. Following the same rationale, lag-2 models were used for fecundity to account for malnutrition or starvation effects on pregnancy as well. Pregnancy lasts about a year in RKW. In addition, and in order to account for cumulative effects of chinook abundance on RKW vital rates, a 5-year running average (chinook abundance from $t-4$ to t) was also used for regression analyses. In total, 128 combinations of stock or stock aggregates, abundance type, and time lag were considered in the analysis of RKW–chinook interactions. Since some of these stock-abundance type-time lag combinations were explored in relation to both NRKW and SRKW (see Box 1), 196 RKW–chinook linkages were analysed: 28 for hypothesis 1a, 60 for 2a, 40 for 1b, and 68 for 2b. Each one of these linkages encompasses relationships with the fecundity and survival of stages directly contributing to population growth, thus producing in total 980 RKW–chinook interactions (Supplementary Material, Appendix S3). The Holm–Bonferroni correction (Holm, 1979) for multiple comparisons was used to filter all positive and significant regressions at $\alpha=0.05$. This is a sequentially rejective correction for multiple comparisons that strongly controls the type-I error rate at level alpha and offers a simple

test uniformly more powerful than the simple Bonferroni correction.

Perturbation analysis

The relevance of interactions between chinook abundance and killer whale population viability were based not only on statistical significance but also on their influence on expected population growth rates as quantified by perturbation analyses (Caswell, 2000). The execution of demographic perturbation analyses involved prospective evaluations (Brault and Caswell, 1993; Fujiwara and Caswell, 2001; Vélez-Espino and Koops, 2009a, b) quantifying the relative effects on SRKW and NRKW population growth of interactions between RKW vital rates and chinook salmon abundance within the hypothesis-driven framework in Box 1. Prospective evaluations, based on elasticity analysis, were used to quantify the changes in λ that would result from any specified change in the vital rates. This information can be used to identify potential management targets because elasticities measure the relative influence of vital rates on λ (Caswell, 2000; Vélez-Espino, 2005; Vélez-Espino *et al.*, 2006). Table 1 summarizes Vélez-Espino *et al.*'s (2014) vital rate and elasticity values for both killer whale populations as generated from 1987–2011 census data

Sensitivity of RKW population growth to chinook abundance

Elasticities (ϵ) are partial derivatives of λ that can be computed with reference to small changes to matrix

Table 1. Vital rate values and elasticities for SRKW and NRKW (1987–2011) from Vélez-Espino *et al.* (2014)

Vital rate	NRKW				SRKW			
	Value		Elasticity		Value		Elasticity	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Calf Survival	0.922	0.088	0.044	0.004	0.785	0.284	0.032	0.010
Juvenile Survival	0.972	0.019	0.264	0.034	0.981	0.047	0.235	0.081
Female 1 Survival	0.989	0.012	0.528	0.056	0.985	0.033	0.549	0.145
Female 2 Survival	0.983	0.025	0.138	0.045	0.967	0.054	0.159	0.150
Female 3 Survival	0.883	0.114	0.000	0.000	0.928	0.108	0.000	0.000
Male 1 Survival	0.977	0.028	0.000	0.000	0.969	0.065	0.000	0.000
Male 2 Survival	0.925	0.078	0.000	0.000	0.897	0.145	0.000	0.000
Female 1 Fecundity	0.142	0.046	0.032	0.005	0.116	0.077	0.023	0.010
Female 2 Fecundity	0.101	0.051	0.012	0.002	0.069	0.074	0.009	0.003

M elements (a_{kl} ; Equation (2)) or lower-level parameters such as vital rates (v_i), which usually contribute to more than one matrix element, by applying the chain rule of differentiation (Equation (3)). Similarly, mean elasticities of interactions between individual vital rates and chinook salmon abundance can be computed by extending the chain rule of differentiation to factors influencing the vital rates (Nichols and Hines, 2002). Equation (4) transfers the effect of a change in chinook abundance on a given vital rate (as determined by significant and filtered beta regressions) to effects on population growth (λ).

$$\varepsilon(a_{kl}) = \partial \log \lambda / \partial \log a_{kl} \quad (2)$$

$$\varepsilon(v_i) = \frac{v_i}{\lambda} \frac{\partial \lambda}{\partial v_i} = \frac{v_i}{\lambda} \sum \frac{\partial \lambda}{\partial a_{kl}} \frac{\partial a_{kl}}{\partial v_i} \quad (3)$$

$$\varepsilon(x_{chinook \rightarrow v_i}) = \sum_i \frac{\partial \log \lambda}{\partial \log a_{kl}} \frac{\partial \log a_{kl}}{\partial v_i} \frac{\partial v_i}{\partial x_{chinook \rightarrow v_i}} \quad (4)$$

The term $x_{chinook \rightarrow v_i}$ denotes chinook abundance from specific stocks or stock aggregates interacting with vital rate v_i , and $\varepsilon(x_{chinook \rightarrow v_i})$ denotes the proportional change in λ resulting from a small change in $x_{chinook \rightarrow v_i}$ through its interaction with v_i . The effects of $x_{chinook \rightarrow v_i}$ on more than one vital rate are additive.

These analytical solutions are robust for perturbations up to 30% and occasionally up to 50% (Caswell, 2001). However, non-linearities often exhibited between vital rates and λ (Mills *et al.*, 1999; de Kroon *et al.*, 2000), reduce the accuracy of projections using elasticities for larger perturbations. Hence, prospective perturbation analysis was also conducted by directly perturbing the projection matrices (Ehrlén and 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. Using direct perturbations, two computational variants of the elasticity of interactions were explored. Variant 1 (Equation (5)) completely represents a direct perturbation process whereas variant 2 (Equation (6)) is a combination of vital rate elasticity and direct perturbation:

$$\begin{aligned} & \varepsilon(x_{chinook \rightarrow v_i})_{DP, variant 1} \\ &= \frac{\Delta \lambda}{\Delta x_{chinook}} \\ &= \frac{((\lambda_{after} / \lambda_{before}) - 1)}{((x_{chinook, after} / x_{chinook, before}) - 1)} \end{aligned} \quad (5)$$

$$\begin{aligned} & \varepsilon(x_{chinook \rightarrow v_i})_{DP, variant 2} \\ &= \varepsilon(v_i) \frac{\Delta v_i}{\Delta x_{chinook}} \\ &= \varepsilon(v_i) \frac{((v_{i, after} / v_{i, before}) - 1)}{((x_{chinook, after} / x_{chinook, before}) - 1)} \end{aligned} \quad (6)$$

The term $x_{chinook, before}$ is the chinook abundance from a particular stock corresponding to the mean value of the interacting vital rate, $x_{chinook, after}$ represents the simulated value of chinook abundance that is used to explore the effect of changes in chinook abundance (e.g. through changes in harvest rates) on RKW population growth rates. Thus, λ_{before} and λ_{after} represent the population growth rate before and after a perturbation on the vital rate(s) corresponding to a given change in chinook abundance as per beta regressions, where $(v_{i, after})$ is the vital rate value after the perturbation. Across all significant beta regressions, the two variants generated similar elasticities of the interactions for SRKW and a slight divergence at higher elasticity values for NRKW (Supplementary Material, Appendix S4). Variant 2 was used for subsequent analysis because it is better suited to incorporate uncertainty in vital rate elasticities as described below.

Stochastic elasticities were generated through simulations with vital rates represented as random variables. Vital rate annual values from 1987 to 2011 were used to generate their mean and variances for each of the killer whale populations. Simulations generated 5000 random matrices with vital rates drawn from defined probability distributions following Vélez-Espino *et al.* (2014). The beta distribution was used to simulate variation in stage-specific survival (σ_i). This distribution is appropriate for binary events (such as survival) and 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. Population growth rates and vital rate elasticities were calculated for each of the 5000 matrices, and a parametric bootstrap was used to estimate mean stochastic elasticities and their 95% confidence intervals.

Sensitivity of RKW population viability to chinook abundance

Future population dynamics, including probability of recovery and extinction risk, ideally require demographic models because they are the only framework that can integrate the vital rates that determine expected change in population size (Caswell, 2001). Population viability analysis (PVA) was based on demographic simulations of perturbed matrices after changing levels of chinook salmon abundance defined by specific fishing scenarios. Four PVA metrics were computed employing R software (R Development Core Team, 2011) and RAMAS_{GIS} (Akçakaya, 2002): (i) stochastic population growth; (ii) mean abundance τ years in the future, where τ is the damping time; (iii) extinction probability 100 years in the future; and (iv) expected minimum abundance.

The same procedure used to estimate stochastic elasticities was used to compute stochastic population growth and to project future population size. Initial conditions were represented by RKW stage compositions in 2011. Following Vélez-Espino *et al.* (2014), projections of population size were conducted at time horizons large enough for convergence to stable-stage distributions based on population-specific damping times at $z=10$. Damping time is defined as $\tau = \ln(z)/\ln(\rho)$ (Haridas and Tuljapurkar, 2007), where ρ is the damping ratio (a measure of the rate convergence to the stable structure; Caswell, 2001) and z is the number of times the contribution of λ (the dominant eigenvalue of matrix **M**) becomes as great as that of λ_2 (the subdominant eigenvalue).

RAMAS was used to generate interval extinction risks for both populations, computed as the probability that abundance will fall below a range of abundances at least once during the next 100 years, and to calculate the corresponding expected minimum abundance. The expected

minimum abundance is used as an index of propensity to decline (McCarthy and Thompson, 2001), and it represents the average (over all replications) of the minimum population abundance of the trajectory. Input data for RAMAS simulations consisted of a projection matrix of mean values and a corresponding matrix of standard deviations for each modelled RKW population. Mean and standard deviation matrices were constructed from the means and standard deviations of matrix elements from the random 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. 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 population growth driven by chance variation in the actual fates of different individuals within a year, was modelled 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 $F_i N_i(t)$. Fecundity and survival rates were correlated within each modelled 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 (Akçakaya, 2002).

The identification of chinook salmon stocks or stock aggregates with the largest influence on RKW population dynamics was based on the value of elasticities of vital rate–chinook salmon interactions and framed by the hypotheses specified in Box 1. The selection of scenarios for SRKW was guided by the implicit need to improve this population's performance in terms of population size and population growth. Hence, the exploration of fishing scenarios for this population focused on either the maximization of chinook abundance through the minimization of harvest rates or the maximization of vital

rates for SRKW, depending upon which one occurred first. The maximum vital rate values for SRKW were based on this population's observed values: 100% for survival and upper 95% CL for fecundity. The most extreme case of minimization of harvest rates corresponded to fishery closures for selected stock aggregates and abundance type (i.e. ocean abundance or terminal run).

The selection of scenarios for NRKW did not respond to a perceived management objective per se but to the research objective of evaluating this population's response to changes in chinook mortality owing to harvest while gaining insights into the potential effects of large increases in chinook salmon harvest rates. Given the clearly positive population growth in NRKW, the exploration of population responses focused on either halting population growth or maximizing harvest rates, depending upon which one occurred first.

The procedure to translate changes in harvest rates, portrayed by selected fishing scenarios, into PVA metrics entailed four steps. First, 1987–2011 (1986–2010 and 1985–2009 for 1-year and 2-year lagged models, respectively) chinook abundance time series were modified according to the characteristics of fishing scenarios. Second, new time series of target vital rates were generated using beta-regression models. Third, new sets of modified projection matrices were created and mean and standard deviation matrices were constructed. Lastly, stochastic simulations were run to generate the four PVA metrics for the comparison of fishing scenarios.

RESULTS

Influence of chinook abundance on RKW demographic rates

The potential effect on population growth and viability of any significant interaction between chinook abundance and killer whale vital rates would depend not only on the slope of the regression but also on the elasticity of the vital rates involved. In addition, the room to improve a vital rate (e.g. there is little room to improve a

survival rate of 95%) will also factor for positive effects on population growth derived from a given interaction. Moving from statistical significance to potential effects on population growth requires perturbation analyses of those significant interactions between chinook abundance and killer whale vital rates. The slope of the regression determines the net change in a vital rate resulting from a change in chinook abundance but vital rates with larger elasticities will have a greater effect on population growth. In addition, interactions between a specific chinook stock aggregate and more than one vital rate would have an additive effect on population growth (as shown in Equation (4)).

Southern resident killer whales

Seven significant ($P < 0.05$) and positive (slope > 0.0) relationships between chinook abundance and SRKW vital rates were identified after applying the Holm–Bonferroni correction for multiple comparisons (Table 2). Four of these relationships represented interactions with chinook salmon terminal run and corresponded to hypothesis 1a (stronger causation weight-of-evidence) while three represented interactions with chinook salmon ocean abundance and corresponded to hypothesis 2a (weaker causation weight-of-evidence). Five of the seven interactions involved fecundity (two for young reproductive females and three for old reproductive females) and two involved the survival of old reproductive females. Within hypothesis 1a, the strongest interaction (based on statistical significance alone) occurred between the fecundity of old reproductive females and the 2-year lagged terminal run of chinook salmon from Puget Sound stocks (pseudo- $R^2 = 0.164$; $P = 0.0076$), followed by interactions between the Fraser Early⁷/Puget Sound aggregate and the 1-year lagged fecundity of old reproductive females (pseudo- $R^2 = 0.086$; $P = 0.0259$). The interaction between Fraser Late⁸ terminal run and the fecundity of young reproductive females was also significant. Within

⁷Fraser Early refers to the aggregate of spring-run and summer-run chinook stocks spawning in Fraser River tributaries.

⁸Fraser Late refers to the aggregate of autumn-run chinook stocks spawning in Fraser River tributaries.

KILLER WHALE-CHINOOK SALMON INTERACTIONS

Table 2. Summary of positive, significant interactions (beta-regression models after Holm-Bonferroni corrections at $\alpha = 0.05$) between chinook abundance and RKW vital rates directly contributing to population growth. Interactions are grouped by population, abundance type, time lag, and hypothesis

Population	VitalRate	Stock or stock aggregate	Abundance Type	Lag	Slope	Intercept	P-value	Pseudo-R2	Hypothesis
SRKW	Fecundity (Female 2)	Puget Sound	Terminal Run	2	1.29E-05	-5.504	0.0076	0.164	1a
	Fecundity (Female 2)	Fraser Early + Puget Sound	Terminal Run	1	6.15E-06	-5.183	0.0259	0.086	1a
	Fecundity (Female 2)	Fraser Early + Puget Sound	Terminal Run	2	6.10E-06	-5.158	0.0275	0.075	1a
	Fecundity (Female 1)	Fraser Late	Terminal Run	2	6.15E-06	-3.005	0.0327	0.073	1a
NRKW	Survival (Female 2)	WCVI + URB + FL + OC + PS	Ocean Abundance	0	3.79E-06	1.381	0.0027	0.446	2a
	Survival (Female 2)	Coastwide (excluding SEAK)	Ocean Abundance	0	2.06E-06	1.355	0.0028	0.488	2a
	Fecundity (Female 1)	WCVI + URB + FL + OC + PS	Ocean Abundance	2	3.20E-06	-4.060	0.0029	0.155	2a
	Survival (Female 1)	Northern BC	Terminal Run	1	2.86E-05	1.600	0.0016	0.335	1b
Survival (Female 1)	Upper Georgia Strait	Terminal Run	5YA	4.85E-05	3.241	0.0028	0.225	1b	
Fecundity (Female 2)	Lower Georgia Strait	Terminal Run	5YA	5.45E-05	-3.973	0.0062	0.109	1b	
Fecundity (Female 2)	Lower Georgia Strait	Terminal Run	2	4.08E-05	-3.542	0.0072	0.096	1b	
Fecundity (Female 2)	Fraser Early	Ocean Abundance	5YA	9.29E-05	-5.907	0.0020	0.142	1b	
Juvenile_Survival	Puget Sound	Ocean Abundance	1	1.72E-05	2.011	0.0031	0.265	1b	
Fecundity (Female 2)	Fraser Early	Ocean Abundance	1	7.19E-05	-5.123	0.0053	0.108	1b	
Fecundity (Female 2)	Fraser Early	Ocean Abundance	2	7.04E-05	-5.029	0.0064	0.078	1b	
NRKW	Fecundity (Female 2)	FE + PS + FL	Terminal Run	1	4.49E-06	-4.722	0.0012	0.097	2b
	Fecundity (Female 2)	Fraser Early	Terminal Run	5YA	1.25E-05	-4.594	0.0015	0.148	2b
	Survival (Female 1)	Oregon Coastal	Ocean Abundance	0	1.50E-05	3.055	0.0003	0.514	2b
	Survival (Female 1)	Coastwide (excluding SEAK)	Ocean Abundance	1	2.15E-06	2.389	0.0008	0.359	2b
	Survival (Female 1)	Fraser Late	Ocean Abundance	5YA	2.04E-05	1.753	0.0013	0.409	2b

Acronyms: **WCVI**: West Coast Vancouver Island; **URB**: Columbia UpRiver Brights; **FL**: Fraser Late; **OC**: Oregon Coastal; **PS**: Puget Sound; **SEAK**: South-east Alaska; **FE**: Fraser Early.

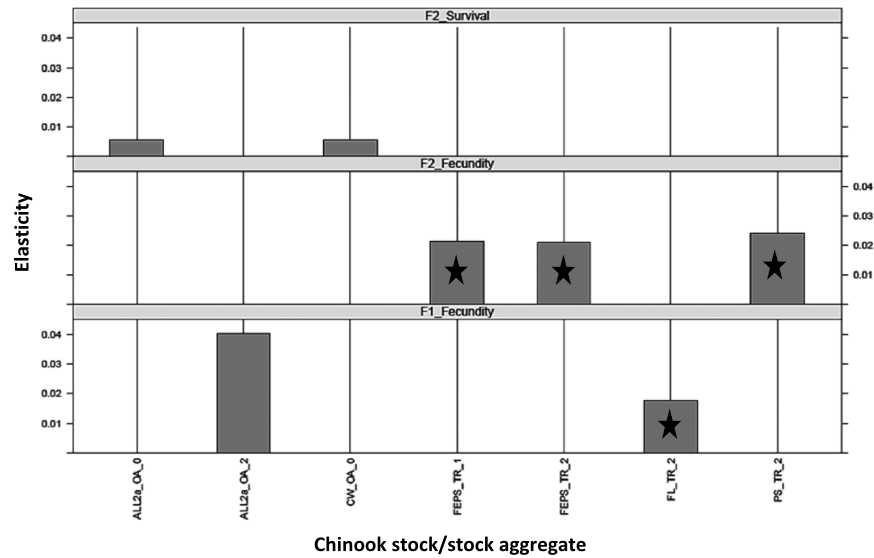


Figure 3. Mean stochastic elasticities of interactions between SRKW vital rates and chinook salmon abundance for all significant regressions in Table 2. Stars indicate interactions under hypothesis 1a. F1: young reproductive females; F2: old reproductive females. **ALL2a**: Five stocks with large contributions to ocean abundance (West Coast Vancouver Island, Columbia Upriver Brights, Fraser Late, Oregon Coastal, and Puget Sound); **CW**: coastwide (excluding south-east Alaska); **FEPS**: Fraser Early/Puget Sound; **FL**: Fraser Late; **PS**: Puget Sound. **TR**: terminal run; **OA**: ocean abundance. Numbers in the stock acronym indicate year lags. See Supplementary Material, Appendix S3 for a glossary of chinook stock abundance definitions.

hypothesis 2a, the strongest interaction occurred between the ocean abundance of the five stocks with the largest contributions to ocean abundance (West Coast Vancouver Island, Columbia Upriver Brights, Fraser Late, Oregon Coastal, and Puget Sound)⁹ and the survival of old reproductive females (pseudo- $R^2 = 0.446$; $P = 0.0027$), closely followed by the interaction between this vital rate and coastwide ocean abundance (all stocks, excluding south-east Alaska) (pseudo- $R^2 = 0.488$; $P = 0.0028$). Additive interactions occurred only once between the aggregate of five large stocks (hereafter 5LSs) and SRKW's old-reproductive-female survival and young-reproductive-female fecundity.

Figure 3, displaying the mean stochastic elasticities of interactions for all SRKW significant regressions in Table 2, shows how interaction elasticities involving fecundity rates were greater than those involving survival of old reproductive females in spite of fecundity rates having vital rate elasticities that are lower than

the elasticities of survival of old reproductive females (see Table 1). This occurs mainly because regression slopes are greater for fecundity than for survival and in some cases because there is more room to improve fecundity than survival. The largest mean elasticity of interactions under hypothesis 1a was that of Puget Sound terminal run and the fecundity of old reproductive females ($\epsilon = 0.024$), closely followed by the interaction between this vital rate and Fraser Early/Puget Sound terminal run ($\epsilon = 0.021$). The largest mean elasticity within hypothesis 2a was that of the interaction between the 5LSs and the fecundity of young reproductive females ($\epsilon = 0.040$), followed by the interaction between coastwide ocean abundance and the survival of old reproductive females ($\epsilon = 0.005$).

The interactions between old-reproductive-female fecundity and the 2-year-lagged Puget Sound terminal run and between this vital rate and the 1-year-lagged Fraser Early/ Puget Sound terminal runs were selected to represent fisheries scenarios pertaining to hypothesis 1a. The additive interaction between the ocean abundance of the 5LSs and both the 2-year-lagged young-reproductive-female fecundity

⁹These stocks have the largest contributions to ocean mixed-stock chinook salmon fisheries managed under the Pacific Salmon Treaty as estimated by the PSC Chinook Model (PSC, 2012).

and the 0-year-lagged old-reproductive-female survival was selected to represent hypothesis 2a. The time series of abundance of these stock aggregates are shown in Supplementary Material, Appendix S5.

Northern resident killer whales

Thirteen significant ($P < 0.05$) and positive (slope > 0.0) relationships between chinook abundance and NRKW vital rates were identified after applying the Holm–Bonferroni correction for multiple comparisons (Table 2). Six of these relationships represented interactions with chinook salmon terminal run and seven with ocean abundance. Eight of the 13 interactions corresponded to hypothesis 1b (stronger causation weight-of-evidence) while five corresponded to hypothesis 2b (weaker causation weight-of-evidence). Seven of the significant relationships were found between chinook abundance and the fecundity of old reproductive females, five involved the survival of young reproductive females, and one involved juvenile survival. Within hypothesis 1b, the strongest interaction (based on statistical significance alone) occurred between the survival of young reproductive

females and the 1-year-lagged terminal run of Northern BC stocks (pseudo- $R^2 = 0.335$; $P = 0.0016$), followed by the interaction between the 5-year running average for Fraser Early ocean abundance and the fecundity of old reproductive females (Pseudo- $R^2 = 0.142$; $P = 0.0020$), and the interaction between the 5-year running average for Upper Georgia Strait terminal run and the survival of young reproductive females (pseudo- $R^2 = 0.225$; $P = 0.0028$). Within hypothesis 2b, the greatest interaction (based on statistical significance alone) occurred between Oregon Coastal ocean abundance and the survival of young reproductive females (pseudo- $R^2 = 0.514$; $P = 0.0003$), followed by the interaction between this vital rate and the 1-year-lagged coastwide ocean abundance, excluding south-east Alaska stocks (pseudo- $R^2 = 0.359$; $P = 0.0008$).

Figure 4 shows the mean stochastic elasticities for all significant regressions in Table 2 related to NRKW. The majority and the stronger interaction elasticities for NRKW involved the fecundity of old reproductive females. The magnitudes of elasticities of interactions for NRKW within hypothesis 1b are comparable with those of hypothesis 2b and also comparable with those observed for SRKW. The greatest interaction

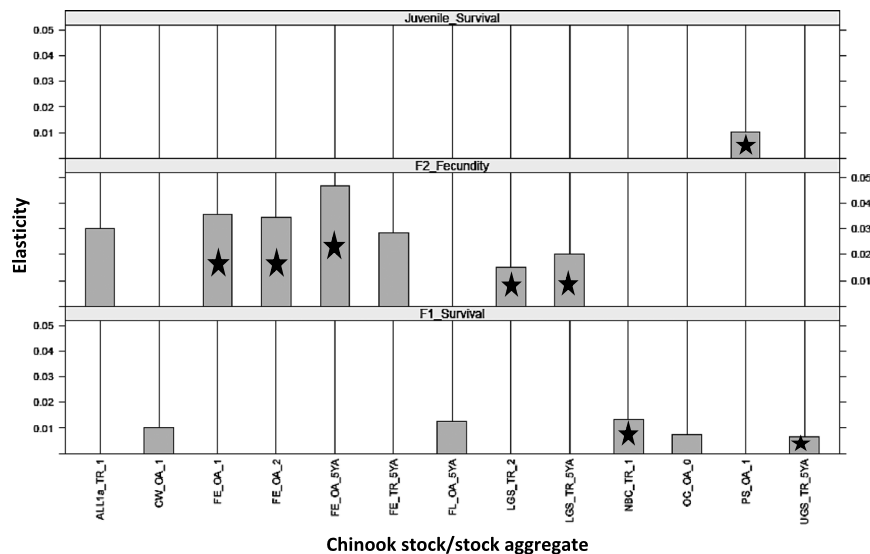


Figure 4. Mean stochastic elasticities of interactions between NRKW vital rates and chinook salmon abundance for all significant beta regressions in Table 2. Stars indicate interactions under hypothesis 1b. F1: young reproductive females; F2: old reproductive females. **ALL1a**: Fraser Early/Fraser Late/Puget Sound; **CW**: coastwide (excluding south-east Alaska); **FE**: Fraser Early; **FL**: Fraser Late; **LGS**: Lower Georgia Strait; **NBC**: Northern British Columbia; **OC**: Oregon Coastal; **PS**: Puget Sound; **UGS**: Upper Georgia Strait. **TR**: terminal run; **OA**: ocean abundance. Numbers in the stock acronym indicate year lags and 5-year running average (5YA). See Supplementary Material, Appendix S3 for a glossary of chinook stock abundance definitions.

elasticities within hypothesis 1b involved Fraser Early ocean abundance (ϵ range: 0.034–0.047), followed by Lower Georgia Strait terminal run (ϵ range: 0.015–0.020), and Northern BC terminal run ($\epsilon=0.013$). Regarding hypothesis 2b, the largest interaction elasticities corresponded to the interactions with 1-year-lagged Fraser Early/Fraser Late/Puget Sound aggregate terminal run ($\epsilon=0.030$) and the 5-year average Fraser Early terminal run ($\epsilon=0.028$), followed by the 5-year average Fraser Late ocean abundance ($\epsilon=0.013$) and coastwide ocean abundance ($\epsilon=0.010$).

The interactions between old-reproductive-female fecundity and the 5-year running average of Fraser Early ocean abundance and between young-reproductive-female survival and the 1-year-lagged Northern BC terminal run were selected to represent fishing scenarios pertaining to hypothesis 1b while the interactions between old-reproductive-female fecundity and the 1-year-lagged Fraser Early/Fraser Late/Puget Sound aggregate terminal runs and between young-reproductive-female survival and the 1-year-lagged coastwide ocean abundance were selected to represent hypothesis 2b. The time series of abundance of these stock aggregates are shown in Appendix S5.

RKW population viability under selected fishing scenarios

Numerous scenarios could be explored to assess effects of changes to chinook salmon harvest rates on RKW population viability, but in light of the relatively small effects of chinook salmon abundance on population growth (as indicated by the low values of the elasticities of interactions), fishing scenarios maximizing benefits to SRKW were explored and, given the clearly positive population growth rate of NRKW, fishing scenarios with the potential to halt NRKW population growth were also explored. Four scenarios were selected for SRKW and five for NRKW, including status quo scenarios (i.e. no chinook interactions; scenarios 1 and 5) as reference. The characteristics and interacting vital rates of these scenarios are shown in Table 3.

Scenarios 2 and 3 were characterized by no ocean fishing on Puget Sound chinook salmon stocks and no ocean fishing on the Fraser Early/ Puget Sound chinook aggregate, respectively, thus maximizing terminal runs of these stock aggregates. In these two scenarios, the elimination of harvest increased SRKW target vital rates but

Table 3. Fishing scenarios selected for the assessment of responses of RKW population viability to changes in chinook salmon mortality owing to harvest. SRKW scenarios explore recovery objectives (i.e. $\lambda > 1.0000$) whereas NRKW scenarios explore halting population growth (i.e. $\lambda = 1.0000$)

Population	Scenario	Hypothesis	Objective	Characteristics	Interacting Vital Rate(s)
SRKW	1	NA	Reference	Status quo	NA
SRKW	2	1a	Recovery	Maximization of PS Terminal Run: no ocean fishing on PS	Increasing the fecundity of old reproductive females
SRKW	3	1a	Recovery	Maximization of FE + PS Terminal Run: no ocean fishing on FE + PS	Increasing the fecundity of old reproductive females
SRKW	4	2a	Recovery	51% reduction in the ocean harvest rates of the five large stocks (WCVI, FL, PS, OC, and URB)	Maximizing the fecundity of young reproductive females and the survival of old reproductive females
NRKW	5	NA	Reference	Status quo	NA
NRKW	6	1b	Halt Population growth	Maximizing ocean harvest rates of Fraser Early chinook	Reducing the fecundity of old reproductive females
NRKW	7	1b	Halt population growth	Reductions of NBC Terminal Run as a result of increasing NBC ocean harvest rates by 187%	Decreasing the survival of young reproductive females
NRKW	8	2b	Halt population growth	Reductions of FE + FL + PS Terminal Run as a result of increasing FE + FL + PS ocean harvest rates by 180%	Decreasing the fecundity of old reproductive females
NRKW	9	2b	Halt population growth	66% increase of coastwide ocean harvest rates	Decreasing survival of young reproductive females

did not maximize them. Scenario 4 was characterized by the maximization of target SRKW vital rates, which occurred after a 51% reduction in the ocean harvest rates of the 5LSs. Scenario 6 was characterized by the maximization of ocean harvest rates of Fraser Early chinook; this scenario, however, did not halt NRKW population growth. Scenario 7 effectively halted NRKW population growth through reductions in NBC chinook terminal run by 187% increases in ocean harvest rates on this stock. Scenario 8 reduced the terminal run of the Fraser Early/Fraser Late/Puget Sound aggregate through increasing ocean harvest rates by 180%. This increment, however, did not halt NRKW population growth but maximized ocean harvest rates of some of the indicator stocks considered for this stock aggregate (see Appendix S2 for details on indicator stocks). Lastly, scenario 9 halted NRKW population growth through 66% increases in coastwide (excluding south-east Alaska stocks) ocean harvest rates.

Status quo conditions

Under status quo conditions, SRKW stochastic population growth rate was 0.91% annual decline ($\lambda = 0.9909$; 95% CI: 0.9719–1.0081), with mean expected population sizes of 84 in 10 years, 78 in 20 years, 71 in 30 years, and 68 in 35 years (damping time). The extinction risk of SRKW was 49% in 100 years with an expected minimum abundance of 15 individuals. For NRKW, stochastic population growth rate was 1.58% annual increase ($\lambda = 1.0158$; 95% CI: 1.0027–1.0285), with mean expected population sizes of 315 in 10 years, 370 in 20 years,

and 401 in 25 years (damping time). The extinction risk of NRKW was zero in 100 years with an expected minimum abundance of 238 individuals. Table 4 summarizes PVA results for status quo and fishing scenarios.

SRKW strong hypothesis (1a)

The maximization of terminal runs via the cessation of ocean fishing on Puget Sound chinook salmon stocks (Scenario 2) or via the cessation of ocean fishing on the Fraser Early/Puget Sound aggregate (Scenario 3) produced marginal increases in SRKW population growth relative to status quo conditions. These increases were enough to create a slightly positive mean stochastic population growth rate (+0.6%) and halved extinction risk (23%) in Scenario 2, but population growth remained slightly negative (−0.02%) in Scenario 3 with an extinction risk of 32% in 100 years. Extinction risk trajectories generated by scenarios 2 and 3 where more linear relative to status quo conditions that produced a concave trajectory (Figure 5). Trajectories from scenarios 2 and 3 were parallel for most of the abundance range. Projected mean population size 35 years in the future increased to 117 in scenario 2 and to 93 in scenario 3 (Figure 6), with expected minimum abundances in 100 years of 41 and 29, respectively (Table 4).

SRKW weak hypothesis (2a)

Scenario 4, 51% reduction of ocean harvests rates on the 5LSs, maximized both the fecundity of young reproductive females and the survival of old reproductive females, and produced the maximum benefits to SRKW population growth and viability

Table 4. Summary of PVA results for selected fishing scenarios in Table 3

Population	Scenario	Mean stochastic population growth	Mean abundance τ years in the future *	Extinction risk 100 years in the future	Expected minimum abundance during 100-year projections
SRKW	1	0.9909	68	49.3%	15
SRKW	2	1.0060	117	22.8%	41
SRKW	3	0.9998	93	32.4%	29
SRKW	4	1.0180	166	12.9%	55
NRKW	5	1.0158	401	0.0%	238
NRKW	6	1.0009	299	1.9%	162
NRKW	7	1.0000	294	3.2%	158
NRKW	8	1.0064	326	1.0%	194
NRKW	9	1.0000	294	3.0%	160

*Damping times (τ) were 35 years for SRKW and 25 years for NRKW.

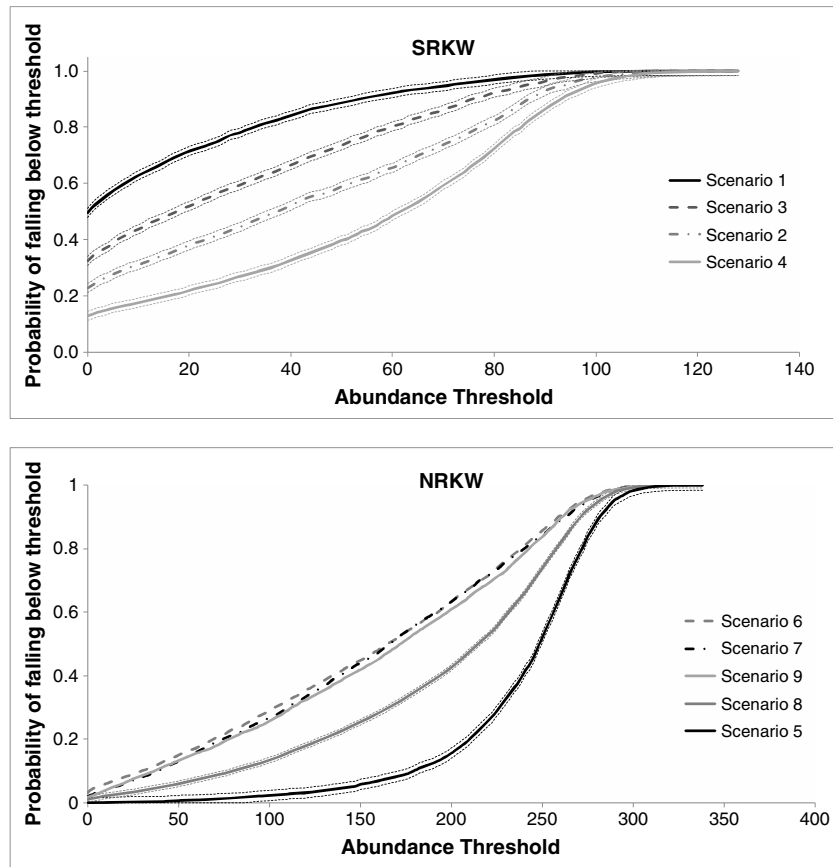


Figure 5. Interval extinction risk for SRKW (top) and NRKW (bottom) under the fishing scenarios in Table 3. These figures show the probability of falling below an abundance threshold in 100 years under environmental and demographic stochasticity. Mean probability (thick lines) and 95% CIs (thin dashed lines) are shown. For clarity, confidence interval lines are not shown for scenarios 6, 7, and 9.

(Table 4; Figure 5). Mean stochastic population growth indicated a 1.80% annual increase with a mean expected population size of 166 in 35 years (Figure 6). The interval extinction risk trajectory was convex for this scenario (Figure 5) and indicated an extinction risk of 13% in 100 years and an expected minimum abundance of 55 individuals during this timeframe. Since this interaction pertains to hypothesis 2a (weak causation weight-of-evidence), any inference is subject to the assumption that the chinook ocean abundances of these five large stocks are important in the diet of SRKW from late autumn to early spring or year-round.

NRKW strong hypothesis (1b)

Regarding hypothesis 1b, ocean harvesting of all Fraser Early chinook (Scenario 6) was not enough

to halt NRKW population growth rate (+0.09%) but it produced an extinction risk slightly greater than zero (2%), and substantially reduced expected minimum abundance (162) relative to status quo conditions (Scenario 5). However, reductions in the terminal run of NBC chinook resulting from a 187% increase in the ocean harvest rates on this stock (Scenario 7), effectively halted population growth and produced an extinction risk of 3% and an expected minimum abundance of 158 in 100 years. This large increase in ocean harvest rates was possible because of the low terminal-run-equivalent harvest rates (average of 19% in the last three decades) on the indicator stock of NBC (see Appendix S2). The trajectories of interval extinction risk in Figure 5 (bottom) were close to linear for these two fishing scenarios relative to the clearly convex status quo trajectory.

KILLER WHALE-CHINOOK SALMON INTERACTIONS

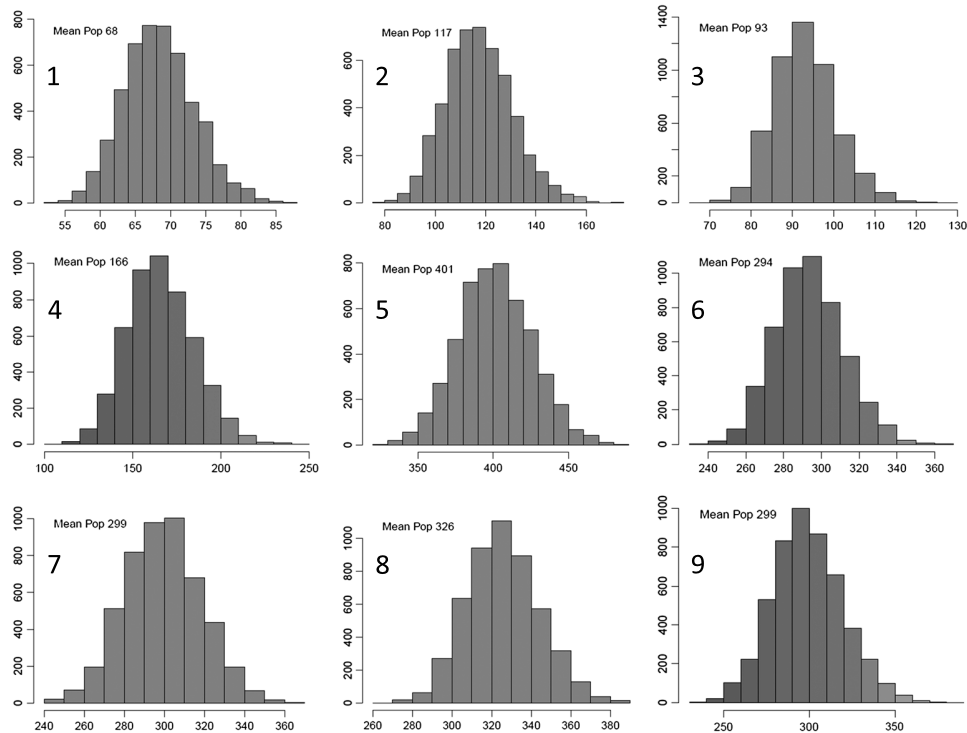


Figure 6. Frequency distribution of population size (5000 realizations) projected under fishing scenarios (1–4 for SRKW and 5–9 for NRKW) in Table 3. Projections are for damping times (τ) of 35 years for SRKW and 25 years for NRKW.

NRKW weak hypothesis (2b)

Scenario 8, reductions in the terminal run of the Fraser Early/Fraser Late/Puget Sound aggregate resulting from a 180% increase in the ocean harvest rates on this aggregate, did not halt population growth (Table 4). Larger increases in ocean harvest rates were not possible since some of the indicator stocks for this aggregate reached 100% at this level. Decreasing the survival of young reproductive females by 66% increases of coastwide ocean harvest rates (Scenario 9) effectively halted population growth. Scenario 8 projected a mean population size of 326 in 25 years whereas scenario 9 projected a mean population size of 299 (Figure 6). The interval extinction risk showing the probability of falling below a given population threshold (Figure 5) indicated an extinction risk in 100 years of 1% for scenario 8 and 3% for scenario 9 with corresponding expected minimum abundances of 194 and 160 individuals, respectively, during this timeframe. The trajectory of interval extinction risk in Figure 5 (bottom) was close to linear for

scenario 9 while scenario 8 exhibited a trajectory that was less convex than the status quo trajectory. Any inference from scenarios 8 or 9 is subject to the assumption that the chinook terminal run of the Fraser Early/Fraser Late/Puget Sound aggregate or chinook coastwide ocean abundance are critical in NRKW diet from late autumn to early spring or year-round.

DISCUSSION

Relative influence of interactions on RKW population dynamics

Linking RKW demographic rates to variations in the levels of chinook abundance necessarily required the simplification of ecological linkages and therefore overlooking many other factors (environmental and anthropogenic) potentially influencing RKW population dynamics. The study of interactions and their demographic effects was possible thanks to the remarkable RKW demographic data and the existence of indices of

chinook abundance representative of their ocean and terminal phases for stocks originating in streams and rivers from northern California to south-east Alaska. And although these indices do not necessarily represent the chinook salmon available for RKW, they represent the best available information to evaluate linkages between chinook abundance and RKW population dynamics. Noticeably, there is indication that these abundance indices are able to capture these linkages at some level because most of the positive and significant interactions between chinook salmon abundance and RKW vital rates involved those stocks identified as predominant in the late spring–early autumn diets of the killer whales, thus providing additional weight of evidence regarding the importance of these stocks for the demographic rates of both SRKW and NRKW.

From the 980 interactions between chinook abundance and RKW vital rates explored herein, 20 were found to be positive and statistically significant. In spite of about twice as many (640 vs. 340) interactions being evaluated for the weak hypotheses 2a and 2b, more than half (12) of the 20 significant interactions corresponded to the strong hypotheses 1a and 1b. The significant relationships between chinook abundance and the vital rates of both SRKW and NRKW under the strong hypotheses 1a and 1b strengthen the case for chinook stocks predominant in the late spring–early autumn diet influencing RKW population dynamics. However, the study revealed that this influence is relatively small. Other factors (genetic, environmental and/or anthropogenic) could be limiting SRKW population growth and possibly masking and confounding the detection of stronger interactions between killer whale vital rates and chinook abundance.

Significantly negative relationships between chinook abundance and RKW vital rates were considered spurious because there is no foreseeable biological (or ecological) mechanism underpinning negative relationships between chinook abundance (the primary food resource of RKW) and RKW vital rates. Even after considering the negative effects of persistent organic pollutant (POP) concentrations in some chinook salmon stocks consumed by RKW (Cullon *et al.*, 2009),

significantly negative relationships between chinook abundance and RKW vital rates would not be the best way of identifying POP effects because prey availability (positive effect) and toxicity load (negative effect) would be confounded. The spurious nature of negative relationships was substantiated in our study by: (1) less than 10% of the significant relationships between stock-specific chinook abundance and RKW vital rates being negative; (2) none involving Puget Sound stocks, which have been identified as having elevated polychlorinated biphenyl (PCB) levels relative to other West Coast populations (O'Neill and West, 2009); and (3) some of these relationships involving chinook salmon stocks for which there is no evidence of heavy POP loads (e.g. Northern BC chinook). Future studies could evaluate relationships between POP levels in chinook salmon tissue and RKW vital rates, in which case the existence of significantly negative relationships would be relevant to support certain hypotheses and quantify the effects of POP on RKW vital rates.

Owing to the relatively low sensitivity of RKW population growth rates to changes in chinook abundance, and therefore changes to chinook mortality due to harvest, the exploration of how different fishing scenarios could influence RKW population viability focused on the maximization of effects. The response of RKW population growth rates to changes in chinook abundance was small even for the interactions with the largest elasticities. The maximum expected change in population growth (based on mean stochastic elasticities), resulting from a $\delta\%$ change in the chinook abundance of a given stock aggregate, never exceeded 0.040 δ in SRKW or 0.047 δ in NRKW. And based on the 95% upper confidence limits of stochastic elasticities, maximum expected changes in RKW population growth rates never exceeded 0.058 δ for SRKW or 0.054 δ for NRKW (Supplementary Material, Appendix S6).

Although interactions were weak on both statistical and demographic grounds, some lent support for causation given the weight-of-evidence regarding the importance of specific chinook stocks in the diet of RKW. Fraser Early and Puget Sound chinook emerged as important under the

strong hypotheses for the two killer whale populations, with the terminal run of these stocks being important for SRKW and their ocean abundance for NRKW. In addition, slightly behind the importance of Fraser Early and Puget Sound stocks aggregates, Fraser Late terminal run was also important for SRKW under the strong hypothesis. On statistical grounds, the relative strength of interactions between NRKW vital rates and both Upper and Lower Georgia Strait aggregates was consistent with the migration routes of these chinook stock aggregates and the preferred feeding areas of NRKW during the summer. Upper Georgia Strait stocks are far-north migrating, spending part of their ocean life in the Gulf of Alaska, and return to their spawning grounds via Johnstone Strait (critical habitat recognized for NRKW; Figure 1), while the Lower Georgia Strait stocks return via both Johnstone Strait and Juan de Fuca Strait (PSC, 2012). Nonetheless, the demographic effect on RKW population growth is greater for the interaction with Lower Georgia Strait stocks because this interaction's regression slope with fecundity is greater than the one with survival characterizing the interaction with Upper Georgia Strait.

Regarding the second type of hypotheses, those that require the assumption that chinook from specific stock aggregates remain important in the killer whale diet year-round and/or outside identified critical habitats, Coastwide chinook ocean abundance (excluding south-east Alaska) was identified as an important stock aggregate common to the two killer whale populations. The 5LSs emerged as important for SRKW but not for NRKW, for which the Fraser Early/Fraser Late/Puget Sound terminal run aggregate had the largest influence. Sampling of NRKW feeding events indicates that Fraser Early chinook returning to their terminal areas are intercepted in the summer months by NRKW in Johnstone Strait and mostly comprise South Thompson chinook (Ford and Ellis, 2006). South Thompson chinook is a summer-run stock that represents the most abundant component of the Fraser Early complex and about 20% of the chinook stocks returning to rivers around the Salish Sea. Fraser Early chinook has a high relative importance in

the diet of resident killer whales in both Johnstone Strait and Juan de Fuca Strait (Parken *et al.*, 2011). In addition, although Puget Sound chinook is also intercepted by NRKW in Johnstone Strait during the summer, Puget Sound chinook are frequently intercepted in Juan de Fuca Strait. Passive acoustic monitoring revealed that NRKW use the southern parts of their range more frequently than previously thought, and highlighted the importance of the southern entrance to the Salish Sea as a RKW hotspot (Riera, 2012). These observations indicate that the summer range of NRKW consistently includes the critical area identified for SRKW (Ford, 2006) and suggest that the relative influence of the Fraser Early/Fraser Late/Puget Sound terminal run aggregate on NRKW population growth under the weak hypothesis may be ecologically substantiated. This could also explain the above-mentioned relative importance of Lower Georgia Strait stocks.

Population viability inferences from selected fishing scenarios

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. The aim of PVAs is not to provide perfect forecasts but to allow comparisons of scenarios under a number of assumptions and considering that as model complexity increases by including additional processes, the increased difficulty of obtaining precise parameter estimates might quickly come to outweigh any perceived advantage of enhanced biological realism (Ludwig and Walters, 1985; Burnham and Anderson, 2002). Within the context of RKW population response to changes in chinook mortality owing to harvest, attention should be placed on the relative differences in population projections under the different selected scenarios rather than on the absolute measures of population size and viability. Some of the factors not included in the PVA that have the potential to increase extinction probabilities and reduce projected population sizes could include indices of climate change, catastrophes, and loss of fitness owing to genetic stochasticity (Lande, 2002). Other

factors that not only add complexity to trophic interactions but may also yield less optimistic population projections include the interactions between chinook salmon and growing populations of other salmon eaters such as harbour seals and sea lions (Preikshot and Perry, 2012).

Within the context of fishing scenarios under the strong hypotheses, the terminal run of Northern BC chinook showed the greatest potential to influence NRKW expected population growth. In the case of SRKW, PVA results showed that equilibrium or slightly positive population growth rates can be produced approximately 50% of the time under extreme reductions to harvest rates such as those resulting from the closure of ocean fisheries targeting Puget Sound and Fraser Early chinook. Surprisingly, larger reductions in extinction risk were identified from the closure of fisheries targeting Puget Sound chinook than from the closure of fisheries targeting both Puget Sound and Fraser Early chinook. These counter-intuitive results just reinforce the finding that the transference of statistical relevance into demographic effects is not straightforward. The interaction with the fecundity of old reproductive females displayed a larger slope for Puget Sound than for the Fraser Early/Puget Sound aggregate. But in terms of demographic effects, histograms of stochastic population growth produced by these two scenarios (Figure 7) show that there is a large overlap between the frequency distributions and the 95% confidence intervals from these two scenarios. Yet, interpretations of these results require the consideration of other lines of evidence, such as diet-composition studies that indicate that Fraser Early chinook makes up a much larger portion of the diet of SRKW in the summer months than Puget Sound chinook (Hanson *et al.*, 2010).

PVA metrics produced by scenario 4, which corresponds to weak hypothesis 2a, produced a much greater increase in SRKW population growth and a greater reduction in extinction risk than other scenarios. This scenario produced a strongly positive annual population growth rate (~1.8%) that, however, remained below the US recovery target of 2.3% (NMFS, 2008). But in spite of the potential this scenario holds to

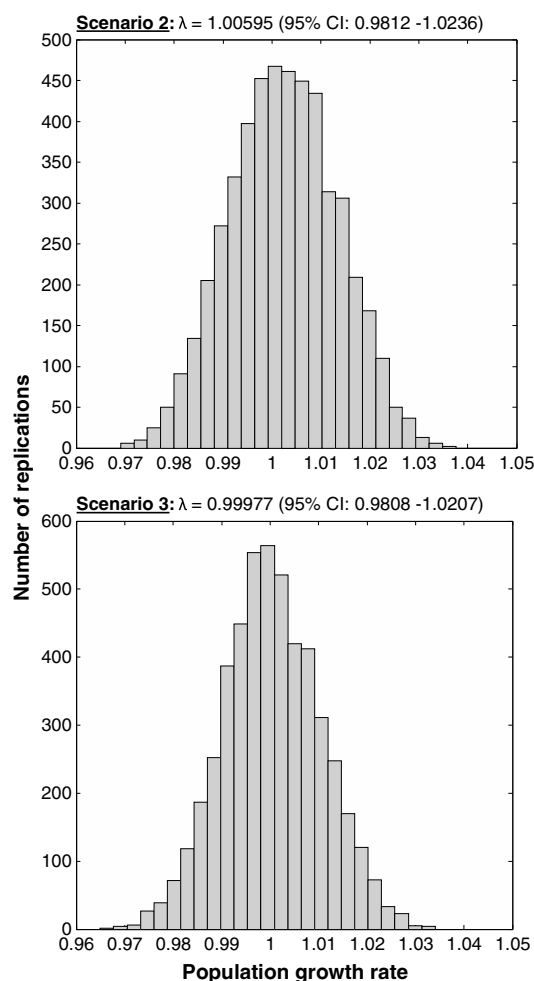


Figure 7. Frequency distribution (5000 replicates) of stochastic population growth for SRKW under fishing scenarios 2 (top) and 3 (bottom). See Table 3 for scenario characteristics.

produce substantial improvement to status quo conditions, it does not represent interactions that have the support of other sources of evidence (such as diet-composition studies) and therefore requires the assumption that the ocean abundance of chinook stock aggregates involved in this interaction (the 5LSs) are important in the diet of SRKW year-round, particularly from late autumn to early spring.

The main benefits of exploring fishing scenarios halting NRKW population growth, or maximizing ocean harvest rates on chinook stocks considered important for this population, have been demonstrating that the population dynamics of NRKW are as sensitive as those of SRKW to

changes in chinook abundance and mortality owing to harvest and showing that there are theoretically feasible levels of chinook mortality due to harvest that can exert large reductions in population growth and even halt the positive trend in NRKW. The possibility that a 66% increase in coastwide ocean harvest rates could halt population growth also means that larger increases in harvest rates could actually cause declining conditions; that is, if key assumptions of weak hypothesis 2b are validated.

Although presently causation cannot be invoked for weak hypotheses 2a and 2b, the results of the PVAs involving these hypotheses have generated new working hypotheses that go from the importance of coastwide chinook ocean abundance on the population dynamics of both NRKW and SRKW to the significance of the chinook terminal run of the Fraser Early/Fraser Late/Puget Sound aggregate or the ocean abundance of Fraser Late stocks or Oregon Coastal stocks (mostly showing the typical northward migration as juveniles) on NRKW population dynamics to the relevance of cumulative effects of chinook abundance levels on RKW vital rates. The main drawbacks of these so called weak hypotheses occur on statistical and ecological grounds. On statistical grounds, it is possible that some of the interactions are spurious and not necessarily representative of predator–prey dynamics. On ecological grounds, there is the possibility of RKW switching to non-salmon prey in months when feeding events have been poorly sampled (late autumn, winter, and early spring). Several decades of RKW studies show, however, that these populations are not generalist predators and raise the possibility that their hunting specialization and prey selectivity can constrain their ability to switch prey in response to scarcity of their preferred prey or to the relative abundances of other prey (Ford and Ellis, 2006; Ford *et al.*, 2010a; Hanson *et al.*, 2010; Williams *et al.*, 2011). Data from a limited number of predation events sampled during winter and spring seem to confirm this prey specialization and selectivity and suggest a prevalence of chinook salmon in the year-round diet of RKW (Ford, 2012).

Management implications

One of the main themes of this investigation has been the sensitivity of RKW population viability to chinook mortality owing to harvest transpiring from interactions between chinook stock aggregates and RKW vital rates. The nature of these interactions has been defined by their weight-of-evidence as determined from diet-composition studies and the probabilities of RKW encountering and preying on specific chinook stocks (Box 1). However, there is a large leap between the identification of relevant interactions – and the characteristics of selected fishing scenarios – and the feasibility or practicality of directing management actions towards those chinook stock aggregates identified as relevant. This is with reference to the difficulty of making harvest rate adjustments to specific chinook stock aggregates in mixed-stock fisheries. Given the highly migratory nature of chinook salmon, ocean fisheries harvest chinook from stocks originating in streams and rivers far away from the area where fisheries are taking place and inescapably intercept chinook salmon from different jurisdictions (Shepard and Argue, 2005). These mixed-stock fisheries are regulated by the Pacific Salmon Treaty and their catch composition is monitored and reported annually. Although genetic data can be used to gain insight into population-specific migration timing (Parken *et al.*, 2008) and hence inform in-season management of chinook salmon (Winther and Beacham, 2009), the current chinook management framework under the PST has not fully incorporated genetic data to assist management strategies for mixed-stock chinook fisheries. It is therefore important to notice that management actions implemented to increase SRKW population growth under current chinook fishery regimes and targeting harvest rate changes for a specific stock aggregate are bound to affect other stocks. Thus, it may not be pragmatic to precisely manage mixed-stock fisheries around specific chinook salmon stocks expecting positive effects on the population dynamics of resident killer whales.

Among the hypotheses explored, the one involving SRKW and chinook stocks evoking greater weight-of-evidence for causation (i.e. hypothesis 1a) is without doubt the most important in terms of

scientific evidence potentially useful to guide management decisions. Interactions under hypothesis 1a involve chinook stocks that are overwhelmingly prevalent in the summer diet of SRKW (Hanson *et al.*, 2010). The SRKW, with its small population size, slightly negative expected population growth and high extinction risk under status quo conditions is in greater need than NRKW of timely management actions directed to improve population viability. The fishing scenarios selected to represent hypothesis 1a essentially imply zero chinook mortality owing to harvest in pre-terminal areas (i.e. closing of ocean fisheries) for Fraser Early and Puget Sound chinook stocks. Scenario 3, which was more consistent with the contribution of Fraser Early to the summer diet of SRKW, basically produces a central tendency to equilibrium ($\lambda \approx 1.0000$). This, however, represents only a marginal increase in SRKW stochastic population growth rate, bounded by large uncertainty (Figure 7), and thus rendering a potential benefit to SRKW population viability that seems to be not commensurate with the scale of such management action.

Final remarks

The continuance of studies of killer whale diet composition in autumn, winter, and spring is deemed essential to substantiate relevant interactions uncovered under the weak hypotheses in this study. This information is critical to avoid potentially spurious correlations and it is required to support causation. Moreover, while chinook salmon represent the majority of the diet of RKW in summer months (Ford *et al.*, 2010a; Hanson *et al.*, 2010), less is known about the seasonal importance of other fish species in non-summer months. Recently, chum salmon (*Oncorhynchus keta*) have been recognized as an important component of the autumn diet (Ford *et al.*, 2010a; Hanson *et al.*, 2010). A study by Vélez-Espino *et al.* (2013) showed terminal runs of Northern/Central BC and Washington chum salmon also covary with RKW vital rates.

Significantly lower calf survival and fecundity of old reproductive females in SRKW than in NRKW were identified as important factors

underpinning the lower population growth and viability of SRKW (Vélez-Espino *et al.*, 2014). A relevant question within the context of this investigation is whether these differences can be explained by linkages between chinook abundance and RKW vital rates. Significant interactions involving calf survival were not found for either SRKW or NRKW. Conversely, most of the significant interactions identified in this study involved the fecundity of old reproductive females for both killer whale populations. The prevalence of this vital rate in the uncovered interactions can be partly due to this vital rate experiencing the greatest variability among vital rates in both populations (Vélez-Espino *et al.*, 2014). Fraser Early ocean abundance interacted with this vital rate in NRKW whereas Fraser Early and Puget Sound terminal runs interacted with this vital rate in SRKW under the strong hypotheses. There are, however, no signs of declining trends in the abundances of Fraser Early and Puget Sound terminal runs (Appendix S5) or evidence of ocean fishery impacts increasing in these stocks. In fact, the relative magnitude of fishery impacts has declined in recent years for these stock aggregates and the same is generally true for chinook salmon stocks coastwide (Vélez-Espino *et al.*, 2013). Thus, lower calf survival and/or lower fecundity of old reproductive females in SRKW cannot presently be associated with different interaction levels with common chinook aggregates, the result of declining trends in the chinook abundance of relevant stocks, or to increasing levels of mortality owing to harvest of these stocks. The possibility of territoriality taking place between SRKW and NRKW and suppressing feeding rates of SRKW on common chinook salmon resources based on the higher abundance of NRKW seems also unlikely. There is no evidence of territoriality in resident killer whales (Ford *et al.*, 2000) or cetaceans in general (Mann *et al.*, 2000). Further research is thus needed to identify the causes of depressed production and survival of calves in SRKW.

Lastly, allocations to predator requirements have been formally considered in the management of some fisheries (e.g. Antarctic krill, North Sea cod) but a challenging scenario occurs when both predator

and prey are endangered (Williams *et al.*, 2011), as is the case with RKW and some chinook salmon stocks identified as important. In spite of the trophic linkages between RKW and chinook salmon evidenced by diet composition studies and the relevant interactions detected in this present study, the results of our analyses also indicate the effects of these interactions on RKW population growth and viability are relatively small (based on hypotheses 1a and 1b) or uncertain and in need of further research (based on hypotheses 2a and 2b). On the one hand, given the current state of information, the conservation status of some of the individual chinook stocks in the Puget Sound and Fraser Early aggregates, and the difficulty to control harvest rates on specific stocks in mixed-stock fisheries, it is highly uncertain whether the allocation of chinook salmon resources for RKW would be an effective management action in RKW recovery plans. On the other hand, large increases in chinook mortality owing to harvest seem to have the potential to produce substantial reductions in RKW population growth (as demonstrated with scenarios 6 and 7 under strong hypothesis 1b), and even halt the markedly positive population growth of NRKW.

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