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A cumulative effects model for population trajectories of resident killer whales in the Northeast Pacific

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ABSTRACT

Like numerous species at risk, the resident killer whale populations of the Northeast Pacific are vulnerable to the cumulative effects of anthropogenic threats. A Pathways of Effects conceptual model summarised the current understanding of each threat (prey availability, acoustic and physical disturbance, and contaminants), threat interactions, and potential impacts to fecundity and mortality. A Population Viability Analysis utilised the most recent available data to quantify impacts of threats on population parameters. The impacts of individual and cumulative threat scenarios on modelled Southern and Northern Resident Killer Whale populations were compared to the observed population demographics to define a model that best captured the real world dynamics. Of the individual and combined threat models tested, the cumulative model incorporating all threats predicted demographic rates closest to those observed for both populations. Recent low Chinook salmon abundance and its interactions with vessel disturbance and contamination strongly influenced modelled killer whale population dynamics. The cumulative effects population viability analysis model projected a mean increase in the modelled Northern Resident Killer Whale population to the carrying capacity within 25 years. In contrast, the mean modelled Southern Resident Killer Whale population trajectory was projected to decline under current conditions, with a 26% probability of population extinction, and in those projections, extinction was estimated to occur after 86 ($\pm$ 11) years. Our results highlight the importance of considering the collective impact of multiple threats to imperilled species and the necessity of testing management and mitigation measures aimed at recovery using a holistic, validated model.

1. Introduction

Effective conservation of species at risk now requires an understanding of the cumulative effects of multiple activities in the ecosystem. The impact of a single threat on a species through time and across its geographical range will always have a degree of associated uncertainty and these uncertainties are compounded when multiple threats co-occur and potentially interact. Uncertainties and interactions among threats make recovery efforts fraught with confusion as decision-makers must consider all evidence to assess potential recovery actions. This balance is demonstrated by killer whale populations around the world that are under threat from several anthropogenic pressures (Desforges et al., 2018; NASEM, 2017). The Southern Resident Killer Whale (SRKW) population is listed as Endangered under the Canadian Species at Risk Act (SARA) and the US Endangered Species Act, and the more northerly but sympatric Northern Resident Killer Whale (NRKW) population is listed as Threatened under the SARA. All populations of Resident Killer Whales are piscivorous, feeding primarily on Chinook (*Oncorhynchus tshawytscha*) and chum salmon (*O. keta*), but despite the similarities in diet and a substantial overlap in range (from southeastern Alaska to Washington State), SRKW and NRKW do not interact with one another socially and are distinct in terms of their culture, acoustics, and genetics (Ford et al., 1998, 2000; DFO, 2017a, 2017b). A comparison of their population dynamics can thus provide insights into the different ways they are affected by human threats (NASEM, 2017).

Long-term photo-identification census surveys for SRKW and NRKW, which were initiated in the 1970s and continue to the present day, show contrasting trends in the two populations (DFO Cetacean Research

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Program; Center for Whale Research, CWR). Population trends based on these census data indicate that the SRKW population has experienced an overall negative population growth rate (−0.002; 1979–2017), with a particularly sharp decline between 1995 and 2001 (Fig. 1). Since then, the SRKW population has shown little recovery, having 73 members as of July 2019. In contrast, the NRKW population has experienced a steady increase over the census period (population growth rate = 0.02; 1979–2017), except for a decline between 1997 and 2001 (Fig. 1). The NRKW population has since increased from 219 members in 2004, to 310 members in 2019 (Olesiuk et al., 2005; DFO, 2020).

The three primary threats to SRKW and NRKW are reduced prey availability, acoustic and physical disturbance, and environmental contaminants (COSEWIC, 2008; Ford et al., 2010; DFO, 2011, 2017a; NMFS, 2008). There is strong evidence that survival and fecundity of these populations are affected by prey availability (Ford et al., 2010; Ward et al., 2009) but limited quantitative evidence on the impacts of disturbance and contaminants. These threats may act on the populations at multiple life history stages and throughout their range. Thus, there is potential for cumulative effects on these populations through repeated exposures to a single threat, exposures at multiple life stages to a threat, and/or exposures to multiple threats. Additionally, threat interactions are known to be common when multiple stressors act within a system (Crain et al., 2008; Darling and Côté, 2008) and non-linear relationships make the effects at a population level difficult to determine. Understanding the effects of cumulative as well as individual threats is therefore necessary to inform the development of effective population conservation strategies (NASEM, 2017).

Several approaches have been used for consideration of cumulative effects on cetaceans. Previous cumulative effects assessments (CEAs) fall into three categories: risk assessment, statistical analysis, and population viability analysis (PVA) (Lacy et al., 2017; Lawson and Lesage, 2012; O et al., 2015). Risk assessment has been used to rank threats and activities of interest occurring in cetacean habitat (Lawson and Lesage, 2012; O et al., 2015). Statistical models have been used to evaluate the impact of single threats on mortality and fecundity of resident killer whales (Vélez-Espino et al., 2015; Ward et al., 2009). A PVA model was developed to evaluate cumulative effects of anthropogenic threats on the SRKW population (Lacy et al., 2017).

The aim of the current assessment is to define and apply a cumulative effects model to evaluate and compare the individual and cumulative effects of anthropogenic threats on both the SRKW and NRKW populations of resident killer whales (after Lacy et al., 2017; Clarke Murray et al., 2019). The study is limited to considering the primary threats identified in the SARA action plan for NRKW and SRKW (COSEWIC, 2008; Ford et al., 2010; DFO, 2011, 2017a, 2018; NMFS, 2008). The definition and testing of an acceptable cumulative effects model will support evaluation of future changes in anthropogenic activities and potential mitigation measures and management actions.

2. Methods

2.1. Cumulative effects assessment

The cumulative effects assessment consisted of two phases: a Pathways of Effects (PoE) conceptual model and a Population Viability Analysis (PVA) quantitative simulation model. The PoE conceptual model described the impacts of threats (or stressors) on killer whale vital rates (mortality and fecundity). As the interaction of threats over space and time can alter their respective intensities and consequent effects on individuals and populations, potential interactions between threats were also assessed to more accurately represent the natural system. The PoE conceptual model consisted of a visual representation of the threat linkage pathways, with supporting justification text (Stephenson and Hartwig, 2009; Government of Canada, 2012) and was developed through literature review and elicitation of expert opinion through consultation with colleagues in relevant fields of expertise.

The outputs of the PoE conceptual model were used to design and refine the structure and parameterisation of the PVA model, building upon the methods and results of previous work (DFO, 2018; Lacy et al., 2017; Taylor and Plater, 2000; Vélez-Espino et al., 2015; Ward et al., 2009; Williams et al., 2017). Existing literature and data were used to parameterise the impact of each threat on killer whale vital rates, and previously published relationships were updated with recent data and re-analysed (detailed in Supplementary Material). The quantitative values and relationships specific to each population (SRKW and NRKW) were used to define the inputs to the population model describing the combined impact on population persistence through time. The model structure builds upon an existing PVA model developed for the SRKW population by Lacy et al. (2017). To capture the unique population structure and threat exposure, a PVA model was developed for each population (SRKW and NRKW) using Vortex 10.3.1, an open access modelling software (Lacy and Pollak, 2014).

2.2. Killer whale population model

Population models were constructed using census data obtained from DFO's Cetacean Research Program encompassing the years 1979–2017 (DFO, 2020; DFO CRP, unpublished data). Annual population surveys have occurred without interruption since 1973 for the NRKW population and 1976 for the SRKW population (DFO Cetacean Research Program; Center for Whale Research, CWR). The SRKW census is considered to be more precise than the NRKW census, as not all members of the Northern

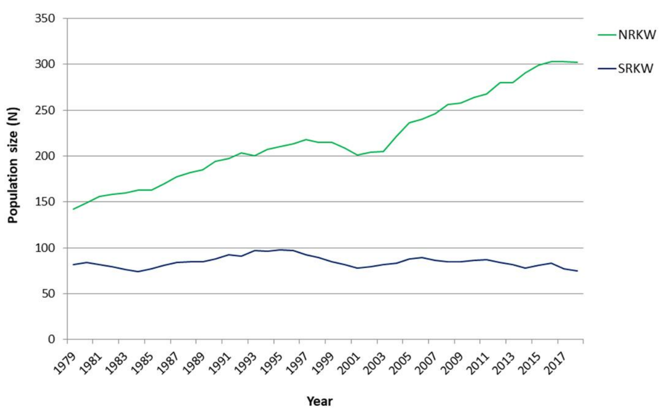

Fig. 1. Resident killer whale population time series, 1979–2018. Source data: long-term photo-identification census surveys for Southern and Northern Resident Killer Whales (SRKW and NRKW), which were initiated in the 1970s and continue to the present day (Fisheries and Oceans Canada Cetacean Research Program; Center for Whale Research).

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population have been seen each year (DFO, 2018, 2020). By using demographic rates starting in 1979 for both populations, the time series is composed mostly of data from direct observations rather than reconstructed data (Olesiuk et al., 2005). The killer whale reproductive system was defined as polygynous and sexually dimorphic with observed population parameters (Table A1; Olesiuk et al., 2005; Vélez-Espino et al., 2014; Ward et al., 2009). Details can be found in Appendix A. The SRKW range extends from southeastern Alaska to central California and the NRKW range from the coastal waters of Glacier Bay (Alaska, USA) to Gray's Harbor (Washington State, USA) (Ford, 2006; Ford et al., 2000).

The neighboring Southern Alaska Resident Killer Whale (SARKW) population has a similar life history strategy but is relatively removed from the threats to which the SRKW and NRKW populations are exposed. The SARKW population has over 700 individuals and has an annual rate of increase considered to be at its maximum, 3.5%, attributed to rebounding salmon stocks (Matkin et al., 2014). The SARKW census data, which began in 1984, were used to define the reference mortality and fecundity rates for the population models, assuming the rates represent those expected from a population in unrestrained growth. The SARKW population is not considered to be pristine as it is exposed to anthropogenic impacts; contaminants and oil spills are the main threats (Matkin et al., 1998, 2014). Notably, a major oil spill (*Exxon Valdez*) occurred in 1989 and resulted in a 33% loss of the resident AB matriline (Matkin et al., 1998, 2008), which has not recovered. However, these anomalous deaths were excluded from the data analysis of Matkin et al. (2008) and do not affect the estimates of vital rates for SARKW used in the present analysis (Table 1). The rates and age/sex structure of the SARKW population were found to be similar to NRKW in their period of unrestrained growth, except that the age of maturity was one year younger for SARKW (Matkin et al., 2008; Olesiuk et al., 2005).

The SARKW vital rates (Table 1) were used in the SRKW and NRKW population models to represent the reference vital rates that determine the growth of each population in the absence of anthropogenic threats. This is an important change from the SRKW model developed by Lacy et al. (2017), where the "baseline" was defined using the mean demographic rates that were observed from recent decades and would therefore include current threat levels. Model scenarios were developed and tested for individual and cumulative threats where threats (described in further detail in later sections) were included in the model as modifiers of the SARKW reference vital rates.

Table 1
Age-specific mortality and fecundity rate for each Resident Killer Whale population: Southern Resident Killer Whales (SRKW), Northern Resident Killer Whales (NRKW) and Southern Alaska Resident Killer Whales (SARKW). SRKW and NRKW data were sourced from Vélez-Espino et al. (2014) for years 1987–2011. SARKW data were sourced from Matkin et al. (2014) for years 1984–2010.

	SRKW	NRKW	SARKW
Age class (y) (male and female combined)	Age-specific mortality rate		
0–1	0.215 (SD = 0.284)	0.078 (SD = 0.082)	0.054 (SD = 0.244)
1–2	0.019 (SD = 0.047)	0.028 (SD = 0.019)	0.003 (SD = 0.040)
2–5	0.019 (SD = 0.047)	0.028 (SD = 0.019)	0.010 (SD = 0.054)
6–10	0.019 (SD = 0.047)	0.028 (SD = 0.019)	0.012 (SD = 0.064)
10–16	0.015 (SD = 0.033)	0.011 (SD = 0.012)	0.008 (SD = 0.032)
17–51	0.033 (SD = 0.054)	0.011 (SD = 0.025)	0.023 (SD = 0.066)
51+	0.072 (SD = 0.108)	0.117 (SD = 0.114)	0.217 (SD = 0.292)
Age class (y) (female only)	Age-specific fecundity rate		
10–30	0.116 (SD = 0.077)	0.142 (SD = 0.046)	0.233 (SD = 0.118)
31–50	0.069 (SD = 0.074)	0.101 (SD = 0.051)	0.154 (SD = 0.118)

2.3. Population viability analysis modelling

The population genealogical and demographic data were partitioned to allow model validation and verification; the complete set of living animals in the year 2000, with their known dams, calving histories, and genealogies, were used as the starting population for each of the population models (SRKW and NRKW). This allowed a comparison of the modelled and observed populations as an evaluation of the ability of the model scenario output data to represent observed data.

Data and knowledge for each of the primary threats were reviewed and statistical analyses updated (see details in following sections). The results of the review and analyses were used to develop single and cumulative threat scenario models.

Model simulations were run on each scenario 10,000 times and summary statistics were recorded for population growth rate (r), population size at each time step (N_t), and probability of extinction (defined as only a single sex remaining). The population size at each year (mean and standard deviation) was compared to the observed (realised) population size for each population from the census survey data. Population growth rate (r) was quantified as the exponential rate of increase, according to the following equation:

$$r = ln\left[\frac{N_{t+1}}{N_t}\right]$$

In long-term simulations that reached an arbitrarily set maximum population size ("carrying capacity", K), the annual growth rate was calculated each year before the truncation of the population size to K, so that the r represented the intrinsic growth that would occur if a ceiling was not imposed on the population size. The model results (the predicted population size resulting from threat-modified reference vital rates) were then compared to the observed (realised) population dynamics from the census data over the same time period (2000–2017). The assumption of this approach is that if a model scenario replicates the realised dynamics for both the SRKW and NRKW populations then the model is appropriate for the system. The inspection approach method was used to validate the models (Law and Kelton, 1991); for the threat-modified model scenarios that most closely approached the observed population parameters, a simulation scenario with historical input data in place of the parameter randomly chosen from a distribution was also evaluated. In this case the yearly Chinook salmon index data was included in the historical scenario. A valid model should closely resemble the observed killer whale survey data when the historical data are used, including population size, age structure and sex ratio.

A sensitivity analysis was conducted on the prey, noise and contaminant parameters in the model to test the impact of uncertainty in these parameters on the results of the study. The sensitivity analysis was conducted in Vortex 10.3 using the Sensitivity Testing operations.

Once a model with acceptable performance was defined, model scenarios were projected into the future to examine the long-term population growth rate and future of the populations. The projection of the cumulative effects model from the 2017 population assumed that the current levels of threats continued into the future, with no changes in threats and no mitigation actions.

2.4. Threats

2.4.1. Prey availability

Field observation and statistical evidence support the relationship between the availability of Chinook salmon and mortality and fecundity rates for these populations (Ford et al., 2010; Ford et al., 1998; Vélez-Espino et al., 2015; Ward et al., 2009). Analysis of prey remains indicates that Chinook salmon can comprise up to 90% of the summer diet of SRKW (Ford and Ellis, 2006; Ford et al., 1998; Hanson et al., 2010).

Ford et al. (2010) reported that SRKW and NRKW survival rates were related to the modelled abundance of Chinook stocks available to six fisheries (Alaska Troll, BC North Troll, BC Central Troll, West Coast Vancouver Island Troll, Georgia Strait Sport, and Washington/Oregon Troll).

The statistical relationship between SRKW/NRKW mortality rates and Chinook salmon ocean abundance index values was updated using the entire time series of SRKW/NRKW and Chinook salmon data (1979–2017). The Chinook salmon stock index that best explains the mortality patterns seen in both populations was tested using model selection (Akaike Information Criterion, AIC). Linear regression was performed between SRKW/NRKW mortality with a one-year time lag and either the Coastwide Index (excluding Southeast Alaska (SEAK) stock, as done in Ford et al. (2000)), or the Chinook salmon runs deemed most relevant to each population (SRKW-stocks and NRKW-stocks). For SRKW-stocks, the WCVI + FL + OC runs were used (West Coast Vancouver Island, Fraser Late, and Oregon Coastal) and for NRKW-stocks the FE + PS + URB were used (Fraser, Puget Sound, and Upper Columbia River Brights) (Table A3) (Stredulinsky, 2016; Vélez-Espino et al., 2015).

To represent prey abundance in the models, Chinook salmon ocean abundance data were obtained from the DFO Salmon Program (A. Vélez-Espino, DFO, Pacific Biological Station) (1979–2017) from the 2018 Pacific Salmon Commission's (PSC) Chinook model calibration. Ocean abundance is an adequate representation of fish available for consumption by killer whales, given that the full time series of terminal run reconstruction data was unavailable, and ocean abundance has statistical support in previous analyses (Stredulinsky, 2016; Vélez-Espino et al., 2015). Yearly modelled ocean abundance was converted to an index of abundance by standardising the value by the mean for the full time series. The Chinook index value was randomly assigned in each model year using a normal distribution as defined by the median value (for a skewed distribution) and standard deviation from the entire time series. Selecting a value from a distribution in each year allowed the model to represent the fine temporal structure and variation in Chinook salmon abundance, and its impacts on killer whale vital rates. The distribution can then be used to project model scenarios over time periods not covered by the historical abundance data.

The availability of prey can also have significant effects on SRKW/NRKW reproductive success and the probability of calving. Ward et al. (2009) assessed calving probability (fecundity) of combined NRKW and SRKW females using a logistic regression model and found that fecundity was highly correlated with the PSC index of Chinook salmon abundance for the WCVI troll and recreational fishery in the prior year (one year lag). The model that best supported the data included age-structured effects on reproduction and a region effect to represent the lower calving rates in SRKW compared to NRKW. The logistic regression analysis was repeated with the additional 10 years of data for calving probabilities and PSC Chinook model ocean abundance salmon indices, following the statistical methods of Ward et al. (2009); additional details can be found in Appendix A. R code for the statistical analyses for prey abundance effects on mortality and fecundity can be found in Appendix B.

2.4.2. Vessel disturbance

Acoustic disturbance (noise) may come from a range of anthropogenic activities but this study focuses on the impacts of vessel-associated disturbance on killer whales. There is limited field evidence on the effects of vessel disturbance. Lusseau et al. (2009) observed a 25% reduction in SRKW feeding activity when boats were present. A noise exposure model combined with a Population Consequences of Disturbance (PCoD) model (National Research Council, 2005; Tollit et al., 2017) estimated that the lost foraging time for SRKW in the Salish Sea from a combination of behavioural responses and acoustic masking due to vessel presence was 20–23% of each whale-day (Tollit et al., 2017). Lacy et al. (2017) assumed that the effect on demographic rates of reduced feeding activity was the same as a comparable reduction in prey (i.e., no behavioural compensation by killer whales). In the PVA model, Lacy et al. (2017) estimated that vessels are present 85% of the daytime and killer whales are foraging in the presence of vessels 78% of the time. This represents a 16.6% reduction in Chinook salmon availability in the model (25% x 85% x 78%).

A time series of vessel activity for the study region that is comparable to the data available for killer whale population dynamics and Chinook salmon was not available. In order to estimate the relative presence of vessels in each population's range, data on the magnitude of vessel presence (commercial, recreational, and whale watching vessels) in the range of SRKW and NRKW were compiled (Appendix A). This estimate was used to set the vessel presence parameter for acoustic disturbance in the model. Acoustic disturbance was modelled as a reduction in feeding efficiency, and was directly linked to the variation in Chinook salmon abundance. The noise parameter was set to 0.85 for SRKW (equivalent to a 16.6% reduction in prey availability) and 1 for NRKW (no effect on prey availability).

2.4.3. Vessel strike

Fatal vessel strikes remove individuals completely from the population, affecting small populations disproportionately. Attributing cause of death in killer whales is difficult in many cases as carcasses often sink and are lost, meaning only a small proportion are recovered for necropsy examination (DFO, 2018; Ford et al., 1998; National Marine Fisheries Service, 2008). Limited data on cause of mortality suggest that SRKW have a slightly higher risk of strike than NRKW, 9.5% and 7.1% respectively between 1979 and 2017 (Appendix A; Baird, 2002; Ford et al., 2000; Williams and O'Hara, 2010). Changes in the frequency of vessel transits and the characteristics of ships (quieter or faster ships may increase strike risk) could affect this probability in the future. The vessel strike threat was modelled as an animal being removed randomly from the modelled adult population once every ten years. The probability was shared equally between males and females of the population.

2.4.4. Polychlorinated biphenyls contamination

The impact of environmental contaminants on killer whale vital rates was investigated using polychlorinated biphenyls (PCBs) as a representative class of contaminants due to a lack of available information on the impacts of other toxins. Hall et al. (2006, 2018) developed a PCB accumulation/depuration model to link PCB levels to calf mortality in cetaceans. The PCB model simulates the accumulation of PCBs in individuals over time, based on a set accumulation rate. Females offload an estimated 77% of their PCB loads to each calf during gestation and nursing (Hall et al., 2006, 2018). This PCB model has been used in cumulative effects assessment for SRKW (Lacy et al., 2017) and in estimating risk to global killer whale populations (Desforges et al., 2018). The dose-response logistic regression model curve used in these studies (Hall et al., 2018) was applied in the PVA scenario models to predict calf survival based on maternal PCB level. Contaminant model scenarios were run using either initial PCB levels from tissue samples summarised by Ross et al. (2000) (1993–1996) or the grand mean for the entire time series of tissue samples (Guy, 2018; Pearce and Gobas, 2018) (Appendix A; Table A10), with three different accumulation rates (1, 2, and 6 mg per year). The modelled PCB concentrations were then compared to the measured PCB levels in tissue samples.

3. Results

3.1. Pathways of Effects conceptual model

The overall PoE conceptual model (Fig. 2a) identified the important conceptual connections between threats (prey availability, acoustic and physical disturbance, and contaminants) and SRKW/NRKW population vital rates (fecundity, mortality), based on literature review and expert opinion. Prey availability appeared to be a central node, with six linkage

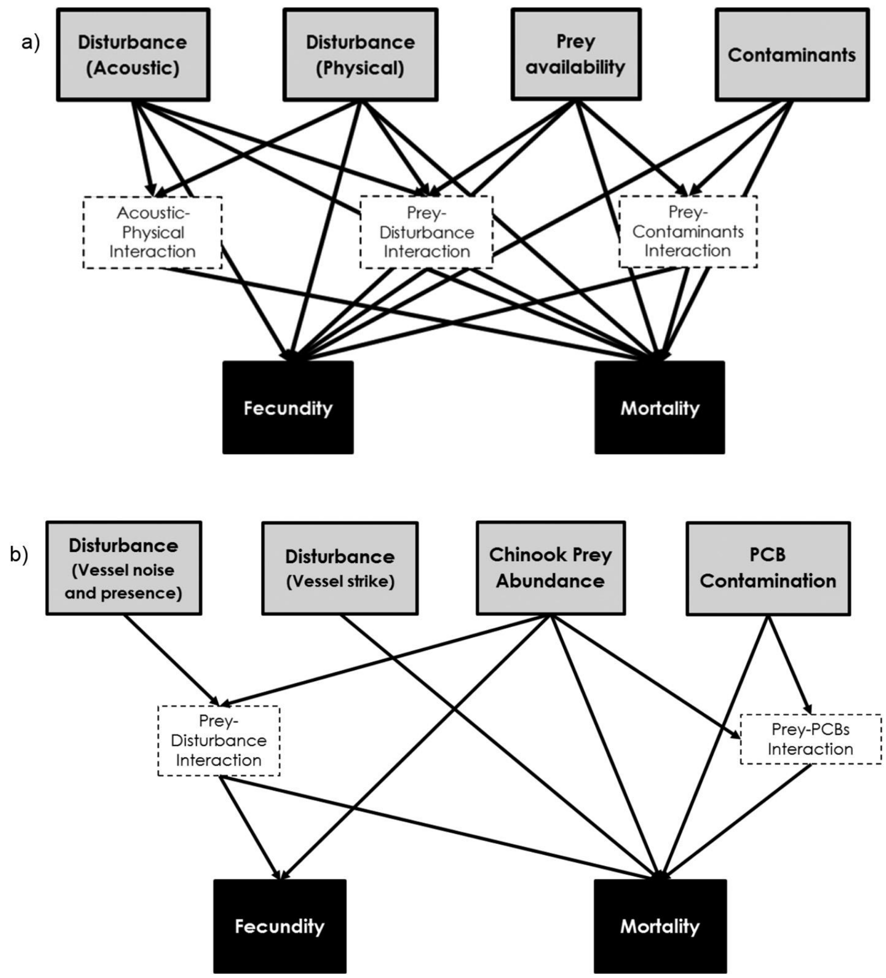

Fig. 2. a) Overall Resident Killer Whale Pathways of Effects conceptual model, including threats, interactions, and impacts on Resident Killer Whale fecundity and mortality and b) Population Viability Analysis model reduced to only the quantifiable threats and interactions.

pathways to fecundity and mortality, including two interactions with other threats (acoustic disturbance, physical disturbance) (Fig. 2a). Interactions make the assessment of impacts more difficult, as they imply that impacts may not be additive and instead may have non-linear or threshold effects. For example, the ability of killer whales to successfully catch and consume prey (access to prey) may be affected by disturbance. The impacts of disturbance could be exacerbated when prey abundance is low, and conversely, disturbance may have little or no effect on overall feeding efficiency when prey abundance is high (Prey-Disturbance Interaction). It has been hypothesised that killer whales might have a higher risk of vessel strike when exposed to loud sounds, which could impair the whales' ability to detect vessels and result in an acoustic-physical interaction effect (Erbe et al., 2018). The effects of PCBs on killer whales may be mediated by nutritional stress and the amount of blubber stores, as observed in seals, resulting in a prey availability-contaminants interaction (Robinson et al., 2018). Blubber-bound toxin levels are higher in Bigg's (transient) killer whales but their population is increasing rapidly (Ford et al., 2007) and therefore may not experience the same toxic effects as in prey-limited populations that are mobilising the toxins during periods of nutritional stress (Mongillo et al., 2016).

Based on the review of the available literature and data, only a subset of the linkages in the PoE conceptual model could be parameterised with empirical data and statistical relationships in the Population Viability Analysis (Fig. 2b). The Disturbance (acoustic) threat was represented by the combined effects of vessel noise and vessel presence as there was no way, with current knowledge, to separate impacts of vessel presence from those of vessel noise. The Disturbance (physical) threat was represented by the effects from vessel strikes. Prey availability was represented by Chinook salmon abundance in the PVA model, even though it is acknowledged that other types of salmon are also consumed. For the Contaminants threat, despite the evidence that other contaminants are present in killer whales, only PCBs could be included.

3.2. Population viability analysis

3.2.1. Threat scenarios

Scenarios for each of the individual threats were constructed and tested using the available knowledge and data (Appendix A). The baseline model using SARKW rates is shown in Fig. 3a. The best fitting statistical relationship between killer whale mortality and Chinook salmon abundance (1979–2017) included the relevant stocks for each killer whale population ($y = 1.6773–0.673\times$; $r^2 = 0.0889$, $p = 0.012$). The previous Ford et al. (2010) analysis used data up to 2003 and the addition of fourteen years of data reduced the explanatory power of the prey-mortality relationship. The best model to explain calving probability (lowest relative AIC value) included the relevant Chinook salmon stocks and an SRKW/NRKW age structure (Appendix A). The percentage of adult females breeding (*Br*) was defined as a logistic function with age structure, using separate parameters for younger (< 31 years of age; Br_1) and older females (> 30 years of age; Br_2). These coefficients were re-

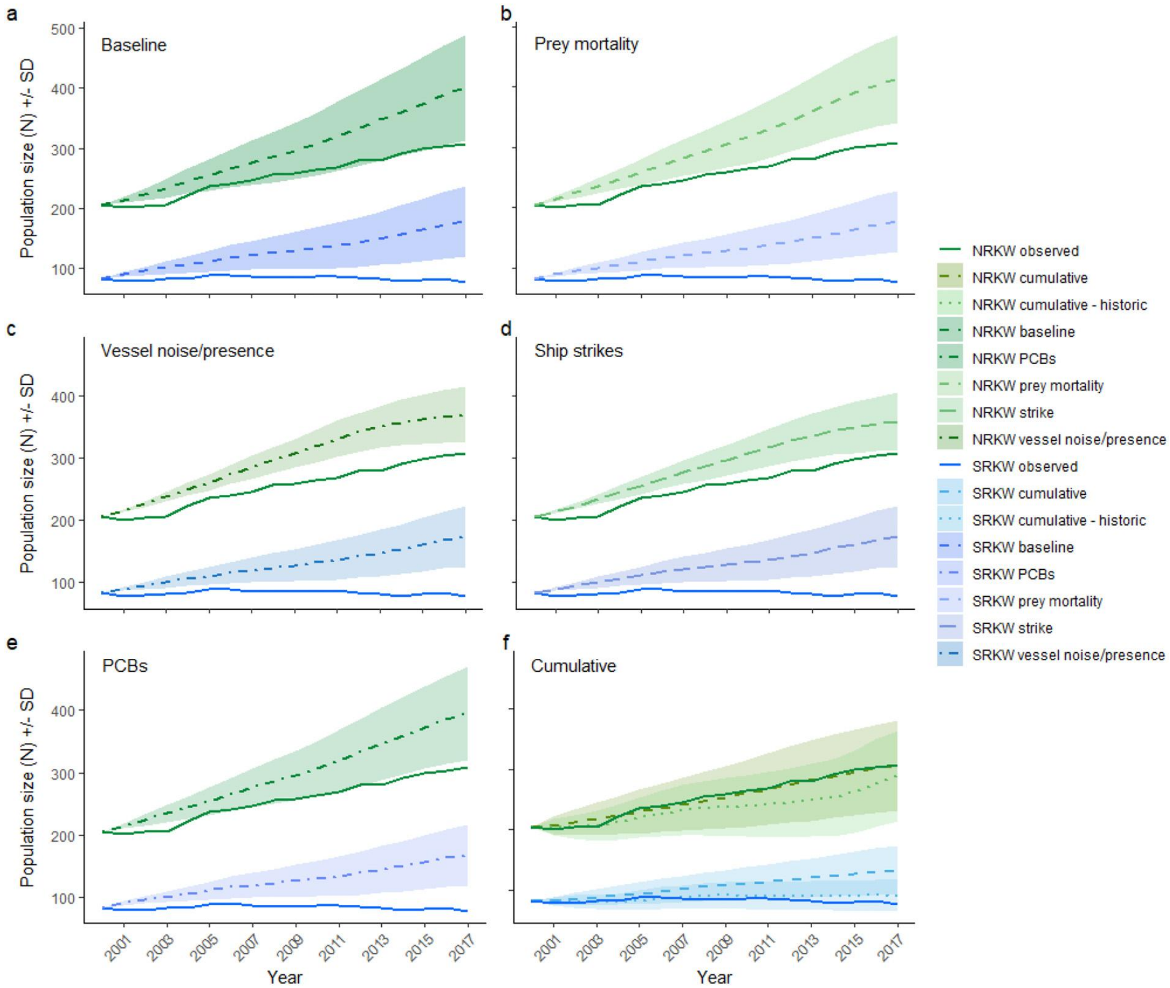

Fig. 3. Mean model simulations of population size (± standard deviation) for single threat scenarios a) baseline, b) prey mortality, c) vessel noise/presence, d) vessel strikes e) PCB contamination, and f) the cumulative effects and historic scenarios (all four threats) on NRKW (green dashed lines) and SRKW (blue dashed lines), with observed population size (solid lines). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

scaled for use in the model scenarios as a reduction to the reference fecundity rate.

In PVA scenario testing, prey abundance effects on mortality alone did not explain the realised population growth (Fig. 3b). The most realistic model for NRKW included the effects of prey abundance on both mortality and fecundity and approached the observed population trend, especially in the first 12 years of the simulation. For SRKW, the model scenario that incorporated impacts on both mortality and fecundity did not match the observed population trend, as it predicted slow population growth, rather than the observed decline. Additional combinations of Chinook stocks and distribution shape scenarios were tested but did not approach the observed population trends (details in Appendix A).

Vessel noise/presence scenarios tested the effect of noise as a reduction in prey abundance, with additional scenarios testing the model for the possibility of a threshold effect where noise affected feeding efficiency only when prey abundance was below the long-term average (Appendix A). None of the vessel noise/presence scenarios approached the observed population dynamics (Fig. 3c). The vessel strike threat scenarios did not match the observed population trends (Fig. 3d). These results suggest that the relatively rare vessel strike threat does not control the dynamics of these populations.

The PCB threat scenario simulations generated a range of mean PCB tissue concentrations in adults across different initial PCB levels and accumulation rates (Table A10). The model scenarios that most closely approached the range of measured PCB levels in recent SRKW/NRKW samples were those with initial PCB levels set to the grand means (SRKW: females = 17.5; NRKW: females = 4.9 mg kg-1 lw), with accumulation rates slightly higher in SRKW than NRKW (2 mg yr^{-1} and 1 mg yr^{-1}, respectively). However, the impact of PCBs alone did not match the observed population growth rate for either population (Fig. 3e).

3.2.2. Cumulative effects

The cumulative effects PVA scenario with all threats included (prey abundance, PCBs, vessel noise/presence and vessel strikes) was closer to the observed population sizes than any of the single threat models (Fig. 3f). The cumulative model included interactions between prey abundance and vessel noise/presence and PCB impacts, where the impact of vessel noise and PCBs was only applied when prey abundance was low (less than the long term mean index) (Table A11). The cumulative model approached the realised population growth for both populations closely, especially in the NRKW population (Fig. 3f). The mean model NRKW population size in 2017 was 309 (± 76 SD) individuals, the recorded NRKW population in 2017 was 308 individuals. The average model SRKW population size in 2017 was 134 (± 41) individuals, and the recorded SRKW population in 2017 was 77 individuals. Using the historical (rather than drawn randomly from the defined distribution) Chinook index values for 2000–2017 resulted in the cumulative effects model approaching the observed population growth even more closely, especially for SRKW (Fig. 3f). Historical values are a useful model validation, but the use of the distribution is needed in order to define a model that can be used for projection into the future.

To further validate the model, we compared the observed and simulated population structure in the cumulative effects model. The relative proportions of juveniles and adults were similar for both SRKW and NRKW (Table A12). The NRKW model was extremely close to the observed values in its outputs (Modelled: 102 juveniles and 207 adults; Observed: 104 juveniles and 204 adults). The observed sex ratios for both populations were also similar to those produced by the cumulative effects models, which both predicted more females than males.

3.3. Model projection

Model scenarios were projected into the future to examine the long-term population growth rate and future of the populations. The projection of the cumulative effects model assumed that the current levels of threats continue into the future, with no changes in threats and no mitigation actions. Future outcomes differed according to whether the full or a subset of the prey abundance time series was used as input to the model. When Chinook salmon abundance was randomly drawn from the long-term mean abundance distribution (1979–2017), the cumulative model projected mean positive population growth for both populations, but with uncertainty among iterations and across years that included negative population growth: 1.6% (± 7.9 SD) for NRKW and 1.5% (± 8.1 SD) for SRKW (Fig. 4). The NRKW population size reached the arbitrarily-set carrying capacity (500 individuals) early in the projections and this affected the projected future population sizes (which would have been higher in the absence of a set carrying capacity). The probability of extinction (defined in the model as only one sex remaining) for both populations was 0% over 100 years. In contrast, when the cumulative effects model used the recent (2008–2017) distribution of Chinook salmon abundance indices the model projected negative population growth for SRKW (−2.5% ± 10.5), and a slightly lowered, but still positive, growth rate for NRKW (Fig. 4). Under the prey scenario using the recent time series, SRKW had a 26.1% probability of extinction and in those simulations where extinction occurred, the mean time to extinction was 86 years (± 11.3 years).

3.4. Sensitivity

The sensitivity of model parameters was tested to distinguish which threats had the highest impact on long-term population dynamics within the model structure. Sensitivity testing was performed for the cumulative effects scenario model projection for SRKW, which includes all four threat variables as well as the defined interactions between disturbance, contamination, and prey availability. The parameter of interest was varied across its range (minimum-maximum) by set increments, with the base values used for all other parameters (Table 2). The base threat levels were the original values used in the cumulative effects model. For the prey parameter sensitivity testing, the full range of Chinook index values for both stocks (1979–2017) was tested (minimum = 0.4, maximum = 1.8). The vessel noise/presence parameter began at the base level of noise (0.85, equivalent to 16.6% reduction in feeding rate) and increased to a maximum of 1.55, to represent the possibilities that either the reduction in feeding time or the time vessels were present could be higher than estimated. Strike risk was varied from 5% to as high as 50%. The PCB value tested included the base initial PCB tissue concentration for females, and included the full range of measured female PCB tissue concentrations. Male PCB tissue concentration was not used in sensitivity testing because the impact pathway occurs via maternal transfer. The most sensitive parameter for the long-term projection of the population was prey abundance (the value of the Chinook index), followed by vessel noise/presence (Fig. 5). Lacy et al. (2017) previously conducted sensitivity analyses on the effect of demographic parameters on population growth in a similar SRKW PVA model and found that variation in fecundity had the strongest effect on population growth for this population.

4. Discussion

The cumulative effects assessment suggests that resident killer whale

Table 2
Parameters and values used for testing sensitivity in the SRKW cumulative effects scenario projection, including the base value, the range, and increment of testing.

Parameter	Base	Minimum	Maximum	Increment
Prey availability (Chinook Index value)	1.00	0.40	1.80	0.10
Disturbance (model value)	0.85	0.85	1.55	0.10
Female PCB tissue concentration (mg kg-1 lw)	17.46	5.00	200.00	25.00
Strike risk (probability)	0.10	0.05	0.50	0.05

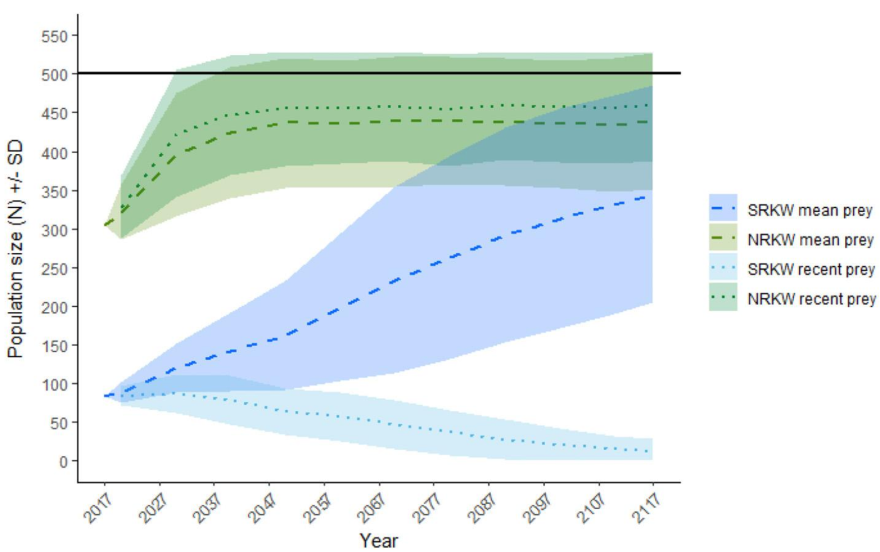

Fig. 4. Mean projection of the cumulative effects model 100 years into the future (starting in 2017) for NRKW (green) and SRKW (blue), under mean Chinook index ("mean prey": 1979–2017) or recent Chinook index ("recent prey": 2008–2017). Error bars represent ±1 standard deviation. Black horizontal line shows the arbitrary carrying capacity set for NRKW (500 individuals). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

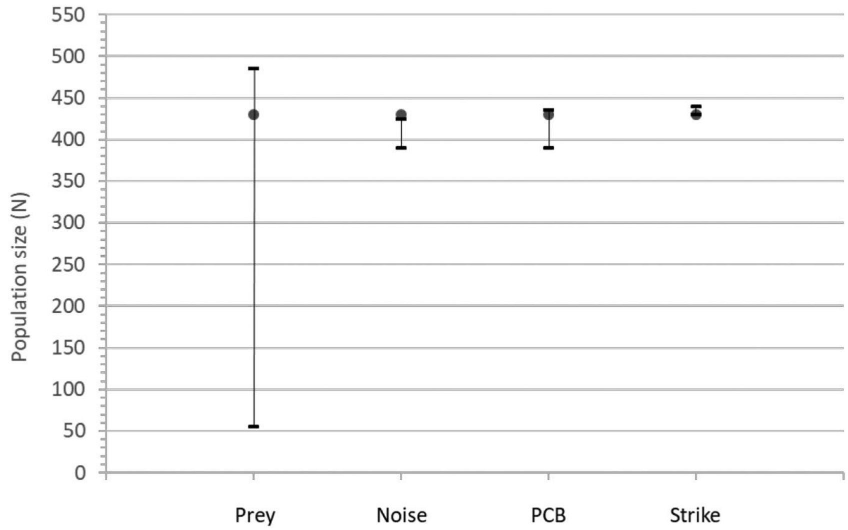

Fig. 5. Sensitivity of SRKW projected population size in the cumulative effects scenario to changes in the threat parameters: prey abundance, vessel noise/presence, PCB concentration and strike risk. Black circles represent the base value for each threat and the vertical bars represent the range of population size (N) with varying threat value (Table 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

populations are affected by the cumulative effect of anthropogenic threats and provides insights into the possible mechanisms behind the two populations' different trajectories. Chinook salmon abundance and its interactions with vessel noise/presence and PCB concentrations strongly influenced modelled killer whale population dynamics, highlighting the importance of considering threats collectively. The cumulative effects model fits the observed data, especially when recent low prey abundances were used, and is a more useful model than single threat models because it includes all threats and therefore can be used to examine tradeoffs in mitigation and management strategies. The cumulative effects PVA model can be used to project NRKW and SRKW population trajectories into the future. These projections are best used in a comparative evaluation of relative outcomes, rather than absolute predictions of abundance.

The projected population growth for both NRKW and SRKW was highly sensitive to the Chinook salmon abundance index. Under long-term mean Chinook salmon abundances, the modelled SRKW population was projected to increase; but when recent, lower Chinook salmon abundances were used, the SRKW population was projected to decline from present-day abundance, with a 26% chance of extinction within 100 years. Model projections were based on an assumption that modelled threat conditions will continue at the same levels as the present day with no mitigation. However, if the Chinook salmon stocks that SRKW depend upon continue to decline, this could affect the future outlook of the SRKW population, and potentially increase the probability of extinction above the model projection.

The findings of this cumulative effects assessment strongly support the significant role of prey availability in determining NRKW and SRKW population trajectories, and are consistent with previous work (Ford et al., 2010; Lacy et al., 2017; Vélez-Espino et al., 2015; Ward et al., 2009). The updated statistical analyses for the effect of prey availability on mortality and fecundity suggest that these impacts are still important to RKW, but the explanatory power of single-threat models has been reduced compared to previous studies. Sensitivity testing showed that prey abundance had the greatest effect on model results, within the bounds of the model structure. Improved mechanistic understanding of the other threats is still needed and could be used to advance the model for projections into the future. The cumulative effects model employed interactions of prey abundance with both vessel disturbance and contaminants, but these mechanisms have not been validated. The most uncertainty among the threats is related to the impacts of underwater noise and vessel disturbance. Additional research is urgently needed on the impacts of vessel presence and noise disturbance on resident killer whales. There are no comparable time series for vessel traffic and proximity to killer whales that would allow similar statistical testing to that done for prey availability. The current work contained a mechanistic model of PCB contamination but other contaminants are also a concern. PBDEs have also been found in high concentrations in these populations (Ross, 2006), although there was insufficient data available to include in the model. An important assumption made in this work is that the pathways of effects from threats to impacts are the same for both SRKW and NRKW; in other words, that the mechanisms by which threats affect individuals are the same for both populations. This assumption is the justification for using the same impact model structure for both populations, albeit with differing threat levels. The consequences of exposure to threats are assumed to be the same for both populations, while the level of exposure to threats is assumed to be population-specific. Differences in distribution, genetics, behaviour and other ecological characteristics at the sub-population (pod/clan) level may affect the exposure to threats and these nuances were not captured in the current assessment. The relationships between threats and resident killer whale mortality and fecundity were determined based on knowledge mostly obtained in the Salish Sea area in the summer/fall period but were assumed to be representative of relationships throughout the entire NRKW and SRKW ranges over the entire year.

Further, the two populations may exploit different prey stocks that themselves have varying population dynamics and availability to killer whale predation. All Chinook salmon stocks went through a period of decline in the 1990s, but since then have experienced stock-specific temporal variation (Ford et al., 2010). The ability and flexibility of killer whale populations to exploit different Chinook salmon stocks, other salmon species and indeed other fish taxa is not fully understood and may vary between NRKW and SRKW and through time. Potential prey competition between the two killer whale populations, and with other marine mammals, such as pinnipeds, may also affect prey availability and has not been included in the current models.

The positive population growth projected by the cumulative effects model under mean prey abundance assumes that the current levels of threats will not increase from present levels, which may not be the case in reality. Changing climate conditions and an increasing human population are having significant ongoing impacts on the marine environment and are likely to continue to affect killer whales and their prey into the future (DFO, 2018; Harley et al., 2006; Walsh et al., 2020). Reductions in threats, such as through mitigation and management actions, may also improve future prospects for positive population trajectories. The USA and Canada have taken a number of management actions in recent years to support the recovery of the SRKW population, including Chinook commercial and recreational fishery closures in key killer whale feeding areas (DFO, 2018). Incorporating the effects of management actions, changing natural conditions, and changes to threat levels into iterations of the cumulative effects assessment may provide useful insights into the potential impacts of these actions on projected population trajectories.

Threats with low probability and high population consequences, such as oil spills or disease outbreaks, are difficult to include in simulation modelling. These threats should not be ignored in management and mitigation because they can have catastrophic consequences if the population were to be exposed. The *Exxon Valdez* oil spill in Alaska was linked to a significant decline in a resident killer whale pod (AB) that had been observed swimming through spilled oil; this pod suffered significant losses in the year following the spill, and had still not recovered to pre-spill levels 16 years after the event (Matkin et al., 1999; Matkin et al., 2008). One way to address high consequence, low probability events such as oil spills in model simulations could be to dramatically reduce the population to 50–75% of the current levels and test if the model population would be resilient enough to recover from such a catastrophe.

This cumulative effects assessment further advances the field by combining a detailed Pathways of Effects conceptual model with a Population Viability Analysis simulation model (after Lacy et al., 2017) to evaluate how the current state of human activities might affect the future persistence of the two imperilled killer whale populations. The incorporation of a PoE model allows the inputs and structure that inform the quantitative PVA to be explicit, and identifies areas lacking knowledge that were not able to be included but could be of value in future iterations. The cumulative effects PVA model could be a useful tool for testing the potential impacts of different theoretical mitigation and management scenarios for individual threats on population trajectories; for example to test whether the complete mitigation of acoustic disturbance would cause the projected population trajectory to increase over time and how long it may take for a change in population trajectory to be observable. Different parameters (e.g., increased vessel presence) can be input into the cumulative effects PVA model to consider the potential impacts of proposed developments and other anthropogenic changes. New information from ongoing and/or planned further research such as prey competition in key foraging areas, foraging efficiency, diet composition, prey field analysis, underwater acoustic monitoring and modelling, and contaminant sources and levels, will all help to inform future iterations of the PoE and PVA models. These models can help to adaptively inform and/or implement recovery measures, such as investigating the benefits of management actions to protect important areas, evaluating potential impacts of disturbance and prey competition from fisheries, assessing the potential impacts of salmon enhancement, and assessing industrial project impacts on killer whales and their habitat to provide advice on avoidance and mitigation measures. Population viability models have been used in conservation biology for over 30 years (Lacy, 2018) with many different approaches. The cumulative effects assessment case study described here builds on this considerable knowledge base and can provide guidance for assessments in other imperilled species.

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CRediT authorship contribution statement

Cathryn Clarke Murray: Conceptualization, Methodology, Formal Analysis, Investigation, Writing-Original draft preparation, Writing - Review and Editing, Supervision. **Lucie Hannah**: Conceptualization, Methodology, Investigation, Writing – Original Draft Preparation, Writing - Review and Editing. **Thomas Doniol-Valcroze**: Conceptualization, Writing – Review and Editing, Supervision. **Brianna Wright**: Investigation, Formal analysis, Writing – Review and Editing. **Eva Stredulinsky**: Investigation, Formal analysis, Writing – Review and Editing. **Jocelyn C. Nelson**: Formal analysis, Visualization, Writing – Review and Editing. **Andrea Locke**: Conceptualization, Writing – Review and Editing. **Robert C. Lacy**: Methodology, Software, Writing – Review and Editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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