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Ranking the relative importance of multiple anthropogenic threats to endangered killer whales to inform effective recovery plans

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ABSTRACT

Understanding the cumulative effects of multiple anthropogenic stressors is key to guiding effective management actions needed to conserve many endangered species. Lack of data makes it difficult to quantify demographic consequences of human activities, which makes it difficult to assess whether management actions are achieving the desired effect. The critically endangered, southern resident killer whale (*Orcinus orca*, SRKW) population of the northeastern Pacific Ocean is an extremely data-rich case study to explore anthropogenic threats. The population's demography has been studied exceptionally well through annual censuses for several decades. The population numbered 79 individuals in three matrilineal social units in 2015. The primary threats are well known, and include: limitation of preferred prey, namely Chinook salmon (*Oncorhynchus tshawytscha*); anthropogenic noise, which may reduce foraging efficiency; and high levels of stored contaminants, including PCBs. We constructed a population viability analysis (PVA), using SRKWs as a case study, to explore demographic stochasticity and the relative importance of three anthropogenic stressors. The detailed, individual-based model of population growth matched observed trends closely. The model found that, because adult survival is already very high in this long-lived species, improvements in fecundity and calf survival are needed to reach one stated conservation objective of sustained annual population growth of 2.3% over a 28-year period. The PVA identified that prey limitation was the most important factor driving population growth rate, followed by anthropogenic noise that would compromise foraging efficiency, and PCB levels. To meet recovery targets, Chinook salmon abundance would have to reach levels higher than observed since the study began in the 1970s. The most optimistic mitigation of any one stressor would make the difference between a declining and increasing population, but mitigating only one stressor alone was insufficient to reach recovery targets. The most pragmatic path to SRKW recovery is to increase Chinook

salmon abundance to the highest levels seen in the last 40 years (i.e., a 25% increase over the long-term average), while simultaneously reducing acoustic disturbance by 50%. Given the number of proposed energy developments that would affect the whales' critical habitat, additional stressors could only worsen a precarious situation for persistence of SRKWs.

INTRODUCTION

As human stressors on the ocean and marine species continue to grow, conservation science is tasked with quantifying the relative importance of multiple anthropogenic threats to endangered species, both to determine whether cumulative impacts exceed sustainable levels and to guide effective recovery plans (Côté et al.; Williams et al., 2016; Wright and Kyhn, 2014). Considerable and rigorous fundamental research is still needed to integrate information on qualitatively different kinds of stressors, which explains why, for the most part, cumulative human impacts are poorly understood and addressed in conservation and management (Maxwell et al., 2013). Such work is need, in part, because threats vary widely in terms of their amenity to mitigation. When regulators require ocean users to forego economic opportunities, these special interests deserve assurance that management actions will help achieve the desired effect of promoting single-species or marine ecosystem conservation (Agardy et al., 2011). One way to accomplish this is to conduct population viability analyses to attempt to rank the relative importance of multiple anthropogenic stressors, in order to direct conservation action toward efforts most likely to promote endangered species recovery (Lacy, 2000). The data necessary to construct fully parameterized models of population consequences of all stressors are not available for most species. Accordingly, a data-rich case study is a sensible way to start.

The fish-eating, southern resident killer whale (SRKW) stock in the northeastern Pacific Ocean is one of the most critically endangered marine mammals found in waters under the jurisdiction of the USA (Reynolds et al., 2009). The USA and Canada have both listed this transboundary stock as Endangered, citing the same three risk factors: lack of the whales' preferred prey, Chinook salmon; chronic and acute forms of ocean noise from shipping, whale watching, and other human activities; and high levels of contaminants, including PCBs (Fisheries and Oceans Canada, 2011; National Marine Fisheries Service, 2008). Management efforts to promote recovery have generally addressed a single risk factor at a time, despite recognition that threats are linked. This has led to widespread perception among some special interests that their sector has been singled out unfairly. To quantify the relative importance of each threat, efforts are needed to integrate simultaneously the best available information on all threats. This will allow managers to target mitigation measures that are expected to provide the greatest conservation benefit to whales at the least cost to ocean users. The biological and environmental data available for Southern resident killer whales are rich by the standards of any marine mammal population. Long-term annual censuses, coupled with a specialized diet, have allowed quantitative relationships to be inferred between prey and various metrics of fecundity and survival (Ford et al., 2010; Ward et al., 2009).

Population Viability Analysis (PVA) uses individual-based demographic models to assess risk to wildlife populations and evaluate the likely efficacy of protection measures, recovery targets, or restoration options (Beissinger and McCullough, 2002; Shaffer, 1990). The Vortex population model (Lacy, 1993; Lacy, 2000; Lacy and Pollak, 2013) is used by thousands of population biologists around the world. Regulatory agencies have used Vortex to set recovery goals and guide actions for threatened and endangered species, including the Mexican wolf (*Canis lupus baileyi* (Carroll et al., 2014)), Florida panther (*Puma concolor coryi* (Maehr et al., 2002)), Sonoran pronghorn (*Antilocapra americana sonoriensis* (Hosack et al., 2002)), Florida manatee (*Trichechus manatus latirostris* (Marmontel et al., 1997)) and many other species. PVA can extend standard demographic projections (Caswell, 2001) in two important ways: (1) the effects of forces external to the population (e.g., habitat degradation; impacts of disease or contaminants; harvest, incidental killing, and other anthropogenic factors) on the demographic rates are explicitly considered and evaluated, and (2) uncertainty in the population trajectory caused by intrinsic (e.g., demographic stochasticity, limitations in local mate availability or other density dependent feedbacks, inbreeding impacts) and extrinsic (e.g., environmental variation, occasional catastrophes) stochastic factors can be explicitly modeled. The outputs of PVA can include a variety of population performance measures, including projected mean population size (N) over time, population growth rates (r), and probability of population extinction. PVA has become a cornerstone of conservation science and resource management. PVA can be used to integrate impacts on individual animals (with respect to mortality, reproduction, and dispersal) into projections of the cumulative consequences at the level of the population, assuming the effects on individuals can be described adequately in the parameters at the level of the model. Deterministic analytical and population-based simulation approaches require that impacts on individuals be accurately captured in consequent changes to a few population-level rates, whereas individual-based simulations let the population-level effects emerge from more detailed descriptions of individual processes.

We constructed an individual-based PVA to model the dynamics of southern resident killer whales using recent demographic parameters. We modeled the sensitivity of our predictions to uncertainty in all demographic parameters, based on inter-annual variability in parameters observed since 1976. We attempted, for the first time, to construct one model that quantifies the population consequences of all three anthropogenic threats to killer whales identified in Canadian and US recovery plans; specifically prey limitation, ocean noise and contaminants. By putting the threats in the same demographic currency, we ranked the relative importance of each by estimating the proportion of variance in population growth rate explained by the three threats. Finally, we used the PVA to explore how much the three threats would have to be mitigated, alone or in combination, to reach a explicit quantitative recovery target for the population in the US, namely sustained population growth of 2.3% over 28 years (National Marine Fisheries Service, 2008).

METHODS

i. Baseline PVA

The PVA modeling of the SRKW population was conducted in three parts. First, a "baseline" model was developed to represent the trajectories of the population if demographic rates remained the same as have been observed in recent decades and if no additional external threats (e.g., oil spills, other environmental contamination, noise disturbance, decreasing food supply, increased disease, increased ship strikes) affected the population. Secondly, uncertain model parameter values were systematically altered to determine which would have proportionately the greatest effects on population projections. This "sensitivity analysis" helps to reveal what confidence we can have in projections (given the necessarily incomplete knowledge of the population characteristics), and which demographic rates are the ones via which the population performance would be most sensitive to any new or worsening threatening processes. Thirdly, estimated effects of additional threats to the population were added to the model to determine which threats individually could put the population at significant further risk and what would be the risk of population decline or collapse under the cumulative impacts of the several identified new threats. Finally, the model was used to explore management and mitigation scenarios, to assess the plausibility of reaching a sustained annual population growth rate of 2.3% given various options for reducing contaminant levels, increasing salmon abundance, or mitigating the effects of ocean noise on foraging efficiency.

The following section describes the modelling approach in general terms. For additional details, including all parameter estimates (and associated measures of variability), please see the Supporting Information material (Appendix 1). In addition, the Vortex project is included in native file format (.XML) in the Supplementary Material. This allows replication of all analyses described in the paper, using the freely available Vortex program.

Primary data source for baseline demographic rates

Demographic rates were calculated from the database on individual animal histories compiled by the Center for Whale Research, using data collected from 1976 through 2014 (unpublished data, 2015). The time series begins when the population was depleted by live-capture fisheries for display in aquaria (Williams and Lusseau, 2006). The time series therefore includes a period of moderate population growth (1976 to 1993), a subsequent decline, and a period of stability or slightly positive growth. Demographic rates were estimated for the same age class groupings used in recent models (Vélez-Espino et al., 2014; Vélez-Espino et al., 2015), except that we set an upper limit for female breeding at 45y rather than 50y. Thus, we calculated survival and (for adult females) fecundity rates for calves (first year), juveniles (defined as from 1 year through 9 years of age), young mature females (10-30 years), older reproductive females (31-45y), post-reproductive females (46y and older), young mature males (10-21 y), and older males (22 y and older). Killer whales can survive many years after reproduce senescence (Ward et al., 2009). We set an upper limit of age to 90y in our models. However, because females stop breeding long before this, the population growth rate will not be affected by the assumed upper age limit. We specified the pod (J, K, or L) of each animal, and assigned each newborn in the simulation to the pod of its mother. We applied the same demographic rates for all three pods. By tracking the membership of each pod, however, we can project the probability that one or more pods will die out.

Mortality rate for each age-sex class was averaged across the 39 years of data to obtain the mean annual rates. The variation in mortality rates across years has two components: 1) environmental variation, and 2) demographic stochasticity. To determine how much of the observed variation is due to environmental variation, the variance due to demographic stochasticity can be calculated from the expectation for a binomial process, and then subtracted from the total variation across years. Calculated annual mortality rates (and environmental variation) ranged from a low of 0.97% (SD=0) for young adult females to 17.48% (SD=17.96) for calves. All inputs are presented in Appendix 1.

The Vortex PVA model

The Vortex PVA model is individual-based, with the fate of each animal tracked through its lifetime. We started the projections of population dynamics with the actual ages and sexes of the killer whales living in 2015. We also specified the mother of each animal, where known (for 76 of 80 living animals; Center for Whale Research, unpublished data; (Ford et al., 2011)). Based on previous data on paternity (Ford et al., 2011), we specified that females would not mate with their father, a son, or a maternal half-sibling (i.e., from the same mother). We used the default option in Vortex to model inbreeding depression as being caused by the presence of recessive lethal alleles.

Reproductive system

The breeding system is polygamous, with some males able to obtain multiple mates, and females mating with different males over their lifetimes. We assumed in the model that males become sexually mature (actively breeding, which may occur several years after they are physiologically capable of breeding) from 12 to 18 years of age. Thus, in the model, each male was assigned an age of sexual maturity by randomly selecting a value from 12 to 18 (assigned when the male was born). Information is available on male mating success (Ford et al., 2011). We incorporated this by assigning each male a score from 0 to 1 as his likelihood of being a capable breeder (i.e., with full access to breeding females) each year. The mean was set at 0.50, with a SD of 0.20 in a beta-distributed distribution (to bound values between 0 and 1). Similarly, we assigned an individual reproductive success score to each female; used to represent the factor by which the female's probability of breeding each year was below (score < 1) or above (score > 1) the overall mean for females of her age. These scores for variation in female reproductive success had mean 1.0 and SD = 0.2, created by sampling from a beta distribution (mean =0.50, SD = 0.1) and doubling those values.

Breeding rates, expressed as the proportion of the females of an age class that produce a calf each year, were calculated from the same time series of annual census data. Rates ranged from 0% for post-reproductive females (age >45) to 12.04% (SD=3.54) for young adult females (age 10-30).

Carrying capacity

For the initial tests of the importance of estimates of demographic rates to the population trajectories, the upper limit on population size was set to 300, so that the "carrying capacity" would not restrict population growth under the best conditions tested. In the projections, the SRKW populations never reached this limiting size. In later analyses of the effects of various threats, carrying capacity was assumed to be K = 150, given that even under optimal conditions, the population growth is not likely to exceed 1.5x the largest population size observed in recent decades. Only rarely did any iteration reach this limit of 150, reducing K from 300 to 150 had minimal effect on the baseline model, and in none of our models did K = 150 restrict growth in more than a few percent of the independent simulations.

Simulation settings

The SRKW population was projected for 100 years with the above input values. The simulation was repeated in 10,000 independent iterations to obtain higher precision in our mean and variance estimations in measures of population performance. For analyses of variants on the input rates (see "sensitivity tests", below) and for comparisons among alternative scenarios, fewer iterations are needed to obtain good estimates of the relative influence of altered input values, and tests of alternative models were run with 1,000 iterations of the simulation.

Sensitivity tests

To determine the sensitivity of the model projections to the uncertainty in 11 demographic input variables, we ran 100 iterations each of 1,000 combinations of input parameters sampled from ranges. The sampled parameters were evenly spaced across the range set for each, with the sampling done according to a "Latin hyperspace" design so that the combinations of the 11 rates were evenly distributed across the entire dimensional space. This method of sampling provides high statistical power for determination of the effect of each parameter.

We modelled sensitivity of ± 10% around eight of the parameters: Birth rate; Annual variation in birth rate; Calf mortality rate; Annual variation in calf mortality; Juvenile mortality rate; Annual variation in juvenile mortality; Adult mortality rate; and Annual variation in adult mortality. We modelled sensitivity of Male and Female variance in Reproductive Success with a SD of 0 to 0.4. We modelled sensitivity of the PVA to uncertainty in Inbreeding effects of ± 50% (i.e., Lethal equivalents = 3.145 to 9.435.

ii. Threats

We integrated data on the three threats identified in the recovery strategies using relationships from previously published studies.

Effects of prey limitation were modelled using previously published relationships linking interannual variability in Chinook salmon to interannual variability in calf and adult mortality (Ford et al., 2010) and fecundity (Ward et al., 2009). The PVA sampled across the entire range of standardized Chinook abundance estimates in the two studies: 1981-2007 (Ward et al., 2009) and 1979-2003 (Ford et al., 2010). We modelled the population consequences of prey availability across the entire range of Chinook abundance metrics (~0.5-1.25) observed between 1979 and 2003. Indices were calculated by dividing the total salmon abundance in each year by its average abundance over the 1979–2004 period (Ford et al., 2010). By definition, a value of 1 represents the average density of salmon over the entire period.

Effects of noise on demography were modelled using the approach outlined in previous analyses of loss of acoustic communication space (Williams et al., 2014; Williams et al., 2016). After selecting a random value for prey abundance in each iteration, a random value representing proportional prey reduction (from 0 to 1) was selected to reduce the proportion of prey available in the environment that was made available to the whale, on average, during the year. Conceptually, this can be thought of as a cumulative acoustic impact score, in which a value of 0.1 represents a foraging efficiency of 90% (1-0.1) over baseline conditions. Because the demographic values have been measured across decades for which ambient noise statistics are not available, any value of proportional prey reduction >0 represents additional noise or disturbance over and above the noise levels SRKWs experienced during the period (1976-2014) when the demographic values were measured. We modelled the population consequences of proportional prey reduction across the entire range of values (from 0 to 100% lost foraging opportunities), and then assessed where empirical estimates of proportional loss of acoustic communication space fell across this range of values (Williams et al., 2014).

Effects of PCBs of calf mortality were modelled using a previously published relationship (Hall and Williams, 2015). The relationship predicts effects of PCB concentrations in lipid on calf mortality, based on meta-analyses of published studies on mink (*Mustela vison*) to quantify a concentration-response relationship in a probabilistic risk assessment. We modelled the population consequences of PCB concentration across a wide range of values (from 0 to 5 mg/kg annual accumulation rate of PCBs), and then assessed where the mean concentration in empirical estimates fell across this range of values (Krahn et al., 2009).

iii. Management and mitigation scenarios

We used the PVA to simulate how much improvement in demographic parameters or how much reduction in anthropogenic threats, singly or in combination, would be required to reach a stated recovery objective of sustained annual population growth of 2.3% for 28 years (National Marine Fisheries Service, 2008). Using the above-mentioned sensitivity analyses, we assessed the relationship between improved demography in three parameters (fecundity, calf survival and adult survival) and population growth rate. Next, we modelled the effects of increased salmon abundance (up to the highest level of the Chinook index observed between 1979 and 2004, namely 1.25 times the average Chinook catch per unit effort relative to the long-term (1979-2004) average. Assuming that current noise levels are sufficiently high to cause foraging efficiency to average 70% (Williams et al., 2014; Williams et al., 2006), we simulated the proportional gain in reproductive rate if acoustic disturbance were eliminated completely (i.e., foraging efficiency reached 100%). Finally, we considered the population consequences of improved calf survival resulting from a complete elimination of PCBs.

RESULTS

i. Baseline PVA

The sensitivity tests in the baseline PVA (Table 1) show that variation in fecundity accounts for most (83%) of the uncertainty in population growth rate. Adult mortality has some influence on the uncertainty in the population trajectories (6.4%), but because these values are already close to 1, there is comparatively little opportunity to improve this parameter. Given the small population size, inbreeding depression may cause sufficient adverse impact on calf survival and population viability (6.1% of the total variance explained) that it should not be ignored in assessments of long-term viability of the SRKW population.

Table 1. Values for each southern resident killer whale demographic parameter used in the PVA's sensitivity analysis, their effect on projected population growth, and proportion of variation explained by variation in that parameter.

Parameter	Baseline	Min tested	Max tested	r-min	r-max	%variance
Inbreeding depression	6.29	3.145	9.435	-0.0005	-0.0029	6.1
Variance in male RS	0.20	0.00	0.40	-0.0017	-0.0023	0.4

Variance in female RS	0.20	0.00	0.40	-0.0017	-0.0019	0.0
Mean birth rate	0.1204 0.0788	0.1084 0.0709	0.1324 0.0867	-0.0062	0.0019	83.0
SD in birth rate	0.0354 0.0415	0.0319 0.0374	0.0389 0.0457	-0.0020	-0.0018	0.0
Calf mortality	0.1748	0.1573	0.1923	-0.0012	-0.0029	3.6
SD in calf mortality	0.1796	0.1616	0.1976	-0.0017	-0.0019	0.0
Juvenile mortality	0.0215	0.0194	0.0237	-0.0011	-0.0028	3.6
SD in juv. Mortality	0.0242	0.0218	0.0266	-0.0015	-0.0019	0.0
Adult mortality	various (see text)	base * 0.9	base * 1.1	-0.0010	-0.0028	6.4
SD in adult mortality	various (see text)	base * 0.9	base * 1.1	-0.0018	-0.0018	0.0

With no improvements, the population is projected to have a marginally negative population growth rate, consistent with what has been observed in recent years (Figure 1).

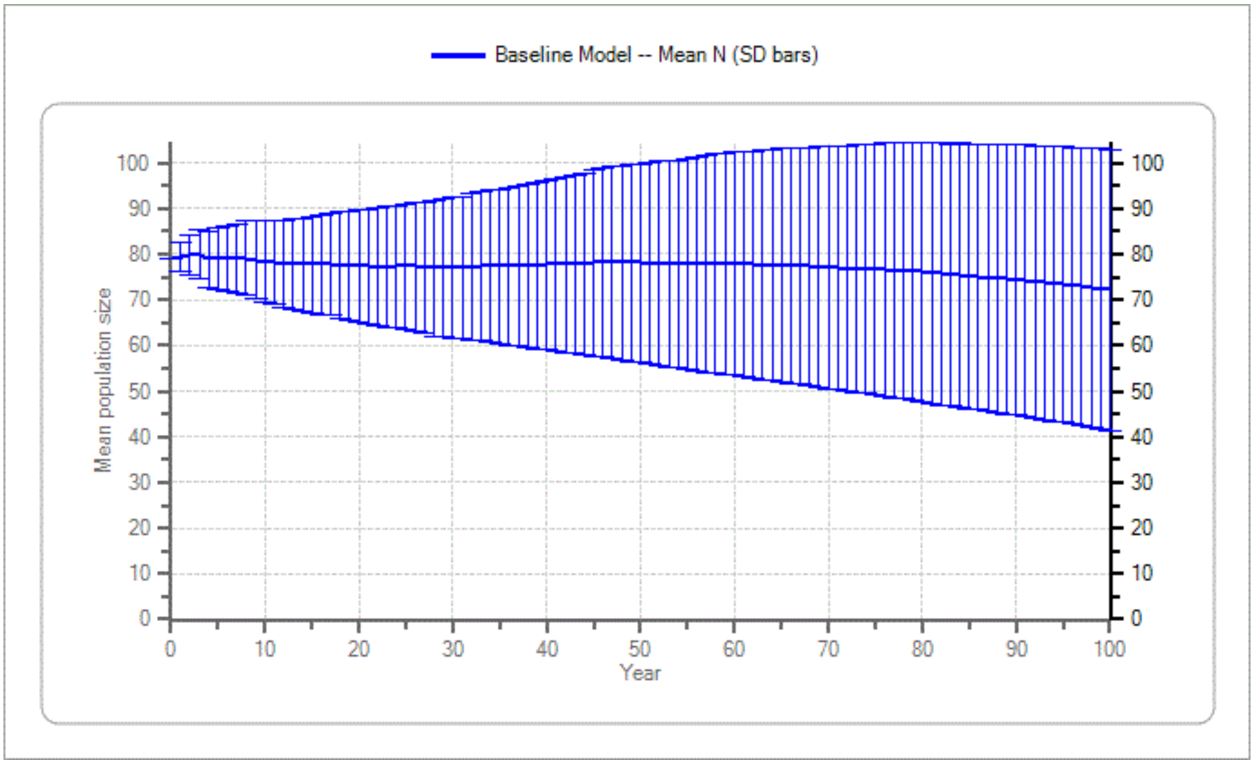

Figure 1. The distribution of simulated trajectories with means and SD of the projected population sizes for SRKWs. Across 10,000 iterations, the baseline model projects a mean population growth rate of r = -0.002 (i.e., 0.2% decline per year), with fluctuation across years of SD(r) = 0.045 (i.e., approximately ± 4.5% growth).

ii. Threats

Of the threats considered, Chinook salmon abundance was found to have the single greatest impact on the population trajectories (Figure 2; Table S2). Although PCB concentrations are high, they are predicted to have relatively little affect on long-term trends in the population. PCB levels are high enough to suppress population growth below 0, whereas without any PCBs the growth would be marginally positive, but the effect is smaller than the other threats considered (Figure 2). Lethal injuries (e.g., bycatch in fishing gear or ship strikes) are rare and expected to have little effect on the population trajectory. Under plausible scenarios (Appendix 1), oil spills may suppress population growth rate (Figure 2).

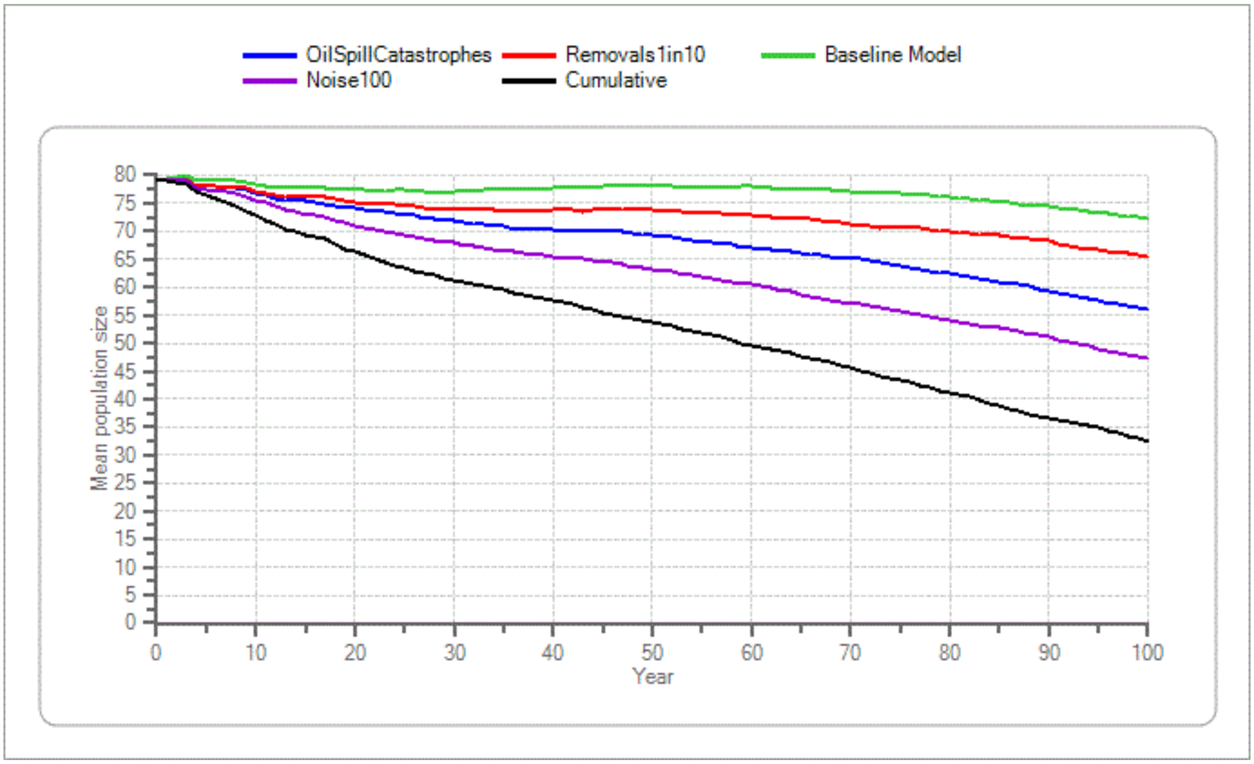

Figure 2. Effects of single stressors, relative to baseline (green line) conditions, on southern resident killer whale population trajectories. Stressors included oil spills (blue line), additional anthropogenic removals (red line), an increase in anthropogenic noise (purple line) and a cumulative effects model that includes all of these stressors (black line).

iii. Management and mitigation scenarios

The demographic analyses showed that it is impossible to reach the SRKW recovery target by improving any single parameter, although increased fecundity would have the greatest positive influence on population growth rate (Figure 3). To reach the stated recovery target, sustained mitigation of threats will be necessary to promote increased fecundity and reduced mortality rates among calves and adults.

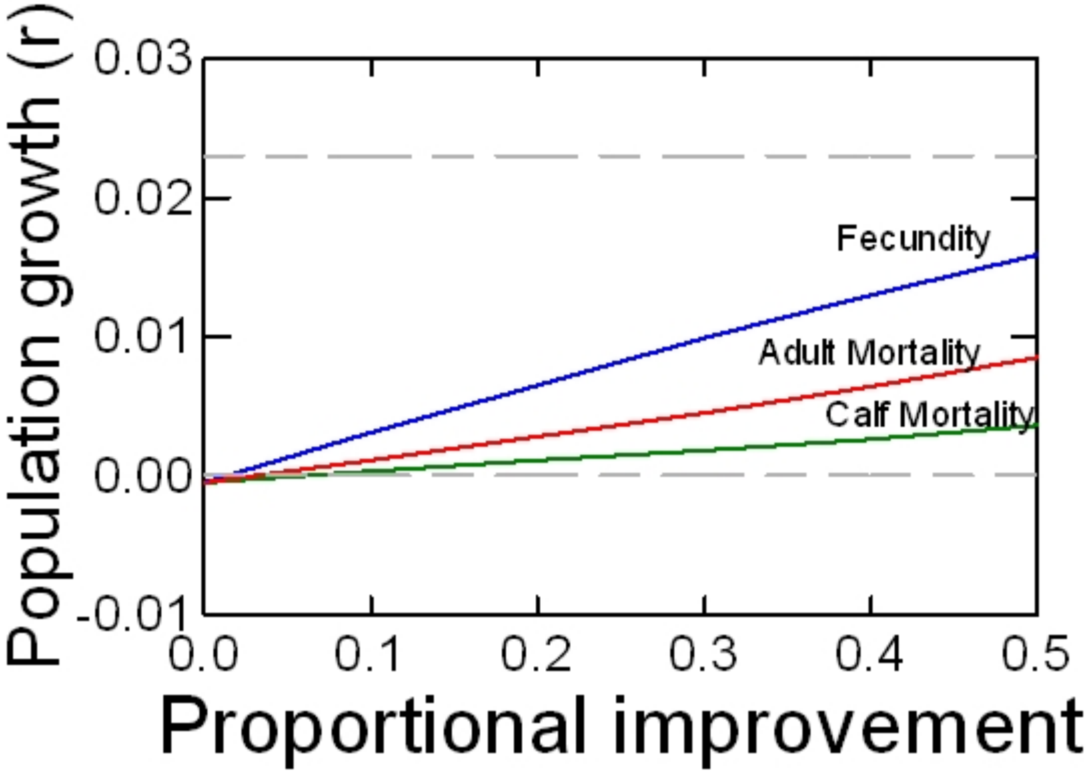

Figure 3. Demographic improvements required to reach one stated SRKW recovery target (dashed horizontal line at 0.023).

The threat analyses showed that it is impossible to reach the SRKW recovery target by mitigating any single anthropogenic threat, although increased Chinook salmon returns would have the greatest positive influence on population growth rate (Figure 4). The PVA estimated that PCBs are causing little impact on this population compared with prey limitation or noise. At current levels, PCBs are expected to suppress population growth slightly below 0, whereas without any PCBs the growth would be marginally positive, but the effect is much smaller than the impact of noise or Chinook abundance. If it were possible to eliminate acoustic disturbance entirely and maintain current levels of Chinook abundance, annual population growth would be expected to reach 1.6%. Complete removal of both acoustic disturbance and PCBs is predicted to cause 1.8% growth. Therefore, reaching the stated recovery target without increasing Chinook salmon numbers is impossible.

The model predicted that a return to the highest rates of Chinook abundance observed between 1979 and 2003 (i.e., 1.25X the long-term average) would cause the population to grow at 2% per year.

Mitigating this threat causes the single greatest increase in population growth, but mitigation of Chinook salmon abundance alone is still insufficient to reach the 2.3% goal. Reducing acoustic disturbance by 50% and increasing Chinook salmon to the highest values observed between 1979 and 2003 would allow the population to exceed the 2.3% growth target, and could cause the population to reach a 3.0% annual growth rate (Figure 4; pink line). A 50% noise reduction plus a 25% increase in Chinook in the environment (i.e., 17.5% increase in Chinook available to the whales) would allow the population to reach the 2.3% target exactly. Other combinations of mitigation are possible.

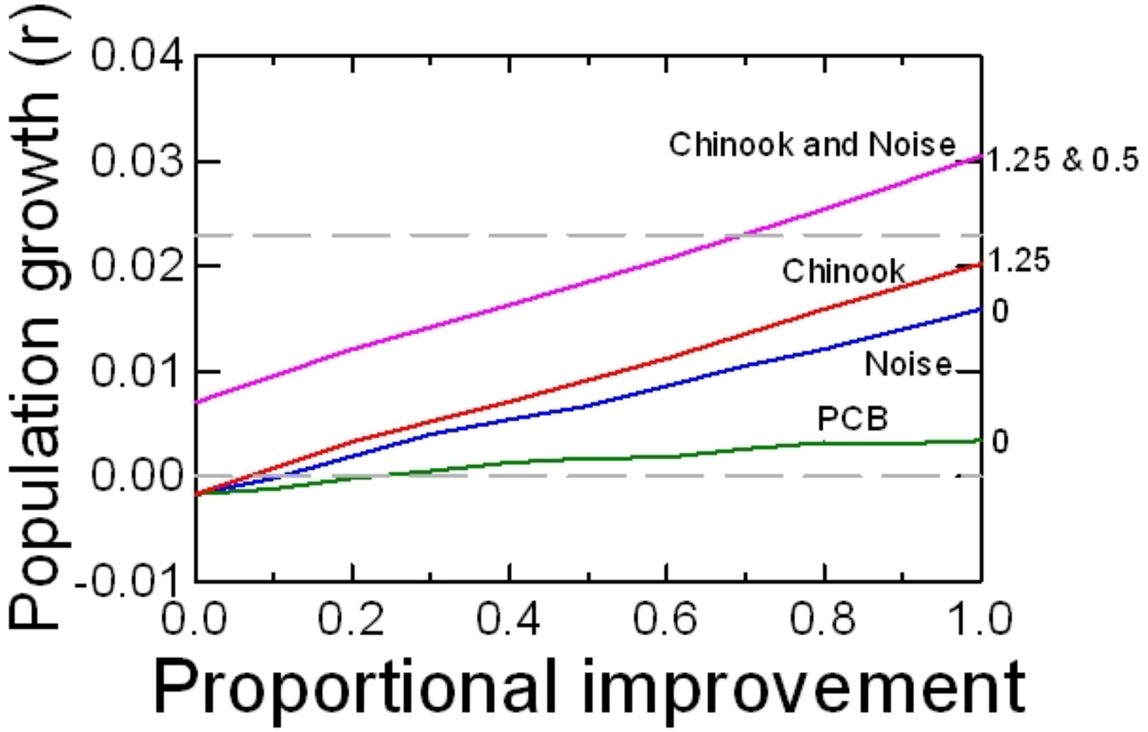

Figure 4. Mitigation of anthropogenic threats required to reach recovery target (dashed horizontal line at 0.023). No single threat can be mitigated to enable the SRKW population to reach a stated recovery target, but that target could be reached with a combination of a 25% increase in salmon returns and a 50% reduction in acoustic disturbance.

DISCUSSION

The SRKW population has experienced almost no population growth during the past four decades, and has declined in the last two decades. Models projecting population changes based on average demographic rates and the fluctuations in those rates across time project that under the status quo the population will most likely remain at about its current size or continue a slow decline. Potential population growth is inhibited in part by the very small size of the population and the consequent lack of available unrelated mates for breeding females. The most important demographic parameter governing population dynamics of SRKWs is fecundity, rather than adult survival. This may seem contrary to conventional wisdom in wildlife population dynamics, but it reflects the reality that adult survival is already high. This finding is similar to a recent comparative study of dynamics of two bottlenose dolphin (*Tursiops truncatus*) populations, which found that interannual variability in reproduction was more important than variability in mortality in describing population dynamics of a long-lived dolphin (Manlik et al., 2016). There is simply more potential for improving reproduction than for improving adult survival in a long-lived species where survival is already close to 1.

The PVA was a useful tool for exploring scenarios relating to the three main anthropogenic threats – prey limitation, acoustic disturbance, and PCBs – that (a) may become worse over time with increased developments in the area, or (b) could be mitigated through management action. Reduction of the Chinook prey base was the single factor projected to have the largest effect on depressing population size and possibly leading to extinction. Occasional large or medium oil spills also can depress long-term average population growth and lead to a considerable chance of the population declining below 30 animals. Progressively lesser impacts were seen with disturbance of feeding by boats, removal (human-cause death) of an animal every 5 years, and small changes in the rate of accumulation of PCBs acquired from the environment.

Our analyses showed that the anthropogenic impacts affecting the dynamics of the SRKW population are linked, and so must mitigation efforts be linked. Reaching the stated SRKW recovery target is impossible by mitigating any single anthropogenic threat alone, although increasing Chinook salmon numbers is an essential component. The PVA is a useful way for managers to identify priorities for future research, and to focus conversations with ocean users and other special interests about the most pragmatic way to promote recovery of endangered species. That discussion necessarily takes place at the science-policy interface, and must integrate discussions about feasibility, cost, societal impact, and timeframe for implementation. If a threat cannot be mitigated in a timescale relevant to conservation of an endangered species, or if its costs are so high that they are prohibitive, thinking of those intractable problems as “fixed costs” in a cumulative impact management framework (Williams et al., 2016) might be useful. For example, our models showed that eliminating PCBs would cause far less benefit to SRKWs than improving salmon returns or reducing acoustic disturbance. This is fortuitous because imagining a way to eliminate PCBs that are stored in a whale's blubber, other than through depuration via lactation, is problematic (Hickie et al., 2007). This focuses attention on mitigating more tractable threats. Identifying fixed costs that are difficult or impossible to mitigate allows a practical discussion about how to allocate the remaining allowable adverse impacts or rank recovery actions among the anthropogenic factors that can be managed.

Of the three threats we considered, the PVA showed that salmon abundance is the greatest factor governing SRKW population dynamics. The model estimated that SRKW recovery cannot be achieved without reaching the highest levels observed since 1979, which represents a 25% higher Chinook salmon abundance than the long-term average between 1979 and 2003. This allows managers to focus discussions on whether that task is attainable, and if so, how to achieve it. Salmon restoration must be the primary focus of action plans, but remaining pragmatic about the timeline and scope is important. For example, removal of an obsolete hydroelectric dam on the Elwha River is expected to increase spawning habitat for all five wild Pacific salmon species in the Salish Sea, but serious discussions about removing the dam began in the 1960s (Witze, 2015) and the cost was in the hundreds of millions of US dollars. There is considerable opportunity to improve growth and survival of wild, juvenile Chinook salmon through restoration of spawning habitat, but this will take money, time, and political will (Sommer et al., 2001). Improvement of marine survival of juvenile Chinook salmon may be possible by containing open-net Atlantic salmon aquaculture sites along the British Columbia coast that host and amplify viruses and parasites that have the potential to reduce survival of wild salmon migrating past the pens (Krkošek et al., 2007; Miller et al., 2011). Reducing Chinook harvest levels may provide a valuable interim opportunity to increase the number of adult salmon available to the whales (Williams et al., 2011), but it is an incomplete measure. Chinook harvests are low relative to the total number of salmon required to promote rapid recovery of the SRKW population (Hilborn et al., 2012).

The most important finding from our PVA is that no single mitigation measure can allow SRKWs to reach the stated recovery target. Both Canada and the US have identified multiple anthropogenic threats to the population (Fisheries and Oceans Canada, 2011; National Marine Fisheries Service, 2008), and management actions to promote recovery must also address multiple threats. The PVA showed that a 50% noise reduction plus a 25% increase in Chinook in the environment would allow the population to reach the 2.3% target. Salmon restoration activities were discussed earlier. Noise is a particularly attractive issue to deal with in a management context, because it lends itself so easily to mitigation. Preliminary calculations suggest that the distribution of source levels of individual ships follows a power law, such that quieting some relatively small fraction of the noisiest ships will reduce noise levels by a disproportionate amount (Leaper and Renilson, 2012). Identifying the noisiest ships operating in SRKW critical habitat (Veirs et al., 2015), and creating incentives to reduce their noise outputs through speed restrictions, maintenance or retrofitting, may offer one way to reduce noise levels dramatically. The International Maritime Organization and the International Whaling Commission have urged member nations to reduce the contribution of shipping to ocean ambient noise, with some countries adopting a pledge to reduce noise levels by 50% in the next decade (Malakoff, 2010). From the perspective of a killer whale, high-frequency noise from whale watching boats that follow whales may be a more important contribution to the acoustic environment than distant ships that raise low-frequency background noise. Management activities that reduce the proximity, number, or speed of commercial or recreational whale watching boats operating around whales may cause greater improvement to a whale's foraging efficiency than changing shipping lanes, which is itself a difficult task (Silber et al., 2012). What is clear is that even without new or increased external threats, the SRKW population has no scope to withstand additional negative pressures. The current situation for SRKWs gives little cause for optimism. This is likely to worsen, given the sheer number of energy-related project proposals for the region, which would increase ocean noise levels and the risk of ship strikes and oil spills (Gaydos et al., 2015).

The case study we present offers an unusual opportunity to examine multiple anthropogenic stressors in a wildlife population that is extremely data-rich by the standard of any marine ecology study (Maxwell et al., 2013). One impact (i.e., the prey-demography links) has been well studied for decades. Another (i.e., acoustic disturbance) is well studied, but requires a conceptual leap to convert straightforward acoustic signal-to-noise ratios to a loss of prey acquisition. The third (i.e., population consequences of PCBs) requires use of a proxy to translate laboratory studies of mink to field studies of whales. This spectrum of from data-rich to data-poor steps in predicting population consequences of multiple stressors is ubiquitous in conservation and ecological studies (Côté et al.; King et al., 2015). The funding to fill knowledge gaps with empirical data may be lacking, or in the case of critically endangered species, there may be insufficient time to wait for science to fill data gaps (González-Suárez et al., 2012). Some authors use expert elicitation (Donlan et al., 2010; Teck et al., 2010) to fill data gaps. The case study presented here illustrates a way to use PVA as an alternative method to inform difficult conservation decisions, by simulating across plausible (or extreme) ranges of uncertainty. For example, sensitivity analyses revealed that some factors (e.g., individual variability in breeding success) have no effect on inference, and such knowledge gaps should not be a barrier to management action. Given the inability to manage insidious threats, such as persistent organic pollutants, it is reassuring to know that the model predicts that this stressor, given no additional information, has relatively little adverse impact on the population. The PVA can focus priority research questions that make a practical difference. Studies of foraging efficiency under varying levels of anthropogenic disturbance, in this example, are needed only because the population is prey-limited. If it were possible to double Chinook salmon numbers, and return them to levels seen in the 1920s (Irvine and Fukuwaka, 2011), it may not be necessary to consider anthropogenic impacts on the whales' foraging efficiency.

Such tradeoffs are all too common in restoration ecology. For example, conservation of grizzly bears (*Ursus arctos horribilis*) in the continental United States focuses on roads and development activities as secondary factors, but the primary concern is that the species was absent from most of its range since the 1800s (Noss et al., 1996). Conservation of an endangered predator, sea otter (*Enhydra lutris*), feeding on an endangered prey species, northern abalone (*Haliotis kamtschatkana*), requires historical perspective that the conflict itself may stem from overharvest of sea otter that continued until 1911 (Chadès et al., 2012). Similarly, the precarious status of southern resident killer whales was not caused by lack of salmon. The root cause of the whales' depleted status was an unsustainable live-capture fishery for display in aquaria (Bigg and Wolman, 1975). Salmon, noise, and contaminants are merely factors that can slow down recovery. Many policies, including the US National Environmental Policy Act require regulators to consider the effect of a proposed activity "which results from the incremental impact of the action when added to other past, present, and reasonably foreseeable future actions regardless of what agency (Federal or non-Federal) or person undertakes such other actions (40 CFR § 1508.7)." Allocating impacts among multiple ocean user sectors may be difficult, but in the case study we present, it is clear that the population is sufficiently imperiled that it has little scope for tolerating additional stressors. Of the world's mammalian species for which data are available, 25% are threatened with extinction (Schipper et al., 2008). We hope that the PVA approach outlined here and the project we made available online, offer a tractable way for conservation scientists to assess the resilience of other populations to current and future anthropogenic threats.

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