Quantifying the effects of prey limitation on killer whale reproduction

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INTRODUCTION

Two populations of fish-eating killer whales inhabit the inshore waters of British Columbia (Canada) and Washington State (USA) and have been listed recently under both the U.S. Endangered Species Act (ESA) and the Canadian Species At Risk Act (SARA). The larger Northern Resident population (listed 2003 under SARA) currently numbers approximately 220 individuals (Fig. 1). The smaller Southern Resident population currently numbers 83. They were listed as endangered under SARA in 2003 and under the ESA in 2006.

We assessed the impact of a wide range of biological and environmental covariates on the fecundity of these two populations, specifically addressing whether fecundity is limited by prey availability (Chinook salmon). Additional variables tested included anthropogenic factors, climate variables, temporal effects, and demographic variables (population size, number of males, female age).

Fig 1. The range of Northern and Southern Resident killer whales.

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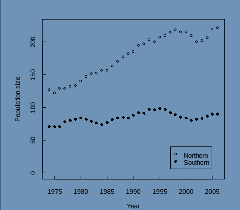

Fig 2. Number of resident killer whales from photographic censuses (for the years of our analysis).

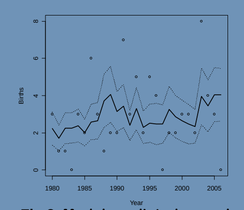

Fig 3. Model predicted annual calves for the Southern Resident killer whales (solid line), 2 se's (dashed lines), and the observed (points);

DATA AND COVARIATES

Population data: Both populations are censused annually using photo-identification techniques. The Southern Resident population has been censused by the Center for Whale Research (Center for Whale Research, 2007). Northern Residents are surveyed by a variety of groups, including the Canadian Department of Fisheries and Oceans (Ellis, Ford & Towers, 2007). Our analysis focused on fecundity, where fecundity is defined as production of a calf that survives to the first survey (after its birth). For 1979-2006, a total 39 Southern Resident females produced 89 calves and 91 Northern Resident females produced 234 calves.

Salmon and other fecundity covariates: As a proxy for the total annual salmon biomass, we used historical indices of Columbia River coho, Columbia River chinook, Washington coho, Washington chinook, and California Central Valley chinook calculated by the Pacific Salmon Commission (PSC).

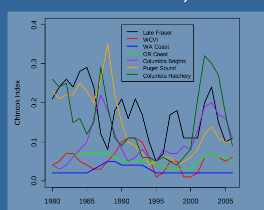

Fig 4. Indices of individual chinook stocks, developed by the PSC.

We also looked for effects of environmental and demographic variables. Environmental variables included the El Niño Southern Oscillation, the Pacific Decadal Oscillation, Northern Oscillation Index, and localized sea surface temperature. The demographic variables included the number of individuals, mature males, and births in the population, matriline and pod.

STATISTICAL ANALYSIS

The response variable in our analysis – whether or not a female produced a calf – was modeled using binomial generalized linear models. In this framework, the response can be written as a non-linear function of covariates;

$$\log(P(\text{birth})/(1-P(\text{birth})) = XB,$$

where the logit-transformed P(birth) is a function of X (a matrix of covariates), and B (a vector of regression coefficients). A model with age and prey as covariates would be, for example,

$$XB=B_0+B_1 age_{i,t}+B_2 age^2_{i,t}+B_3 age^2_{i,t}+B_4 age^4_{i,t}+B_5 prey_i$$

Maternal age was modeled as a 4th order polynomial to allow the rate of maturity and rate of reproductive senescence to be asymmetric. Bayesian and maximum likelihood methods for parameter estimation. We used Bayesian (Bayes factor) and likelihood (AIC) model selection to compare models.

RESULTS

Age of the mother was the strongest explanatory variable. We found that killer whale reproduction follows a pattern seen in other large mammals (Packer, Tatar & Collins 1998): a rapid increase in fecundity followed by a gradual decline and finally reproductive senescence (Fig. 7).

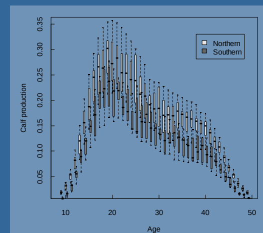

Fig 5. Effect of age on killer whale fecundity.

After controlling for the age of mothers, we found that prey abundance was the strongest predictor of yearly fecundity rates (calves / female). More specifically, it was the index of chinook salmon abundance off the West Coast of Vancouver Island in the previous year that was strongly positively correlated with fecundity (Fig. 6). Following highly productive salmon years, the probability of calving is 50% higher at the population-level compared to years following low salmon years (Fig. 7).

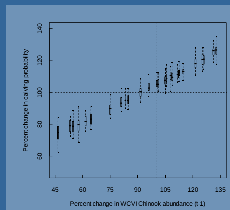

Fig 6. Deviation from the model predicted calving probability as a function of deviation in WVI chinook abundance relative to the 1980-2006 mean.

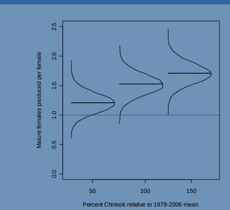

Fig 7. Relationship between the 1-year lagged PSC salmon abundance index and the killer whale production rate.

We found weak evidence for including a regional difference between populations. Inclusion of the regional effect translates into the southern population having slightly lower calving rates relative to their northern counterparts (Fig. 5).

There appeared to be no support for any of the additional covariates, regardless of whether year was treated as a numeric variable or groups of years were treated as factor variables. Killer whale fecundity therefore did not appear to have been affected by variables other than age structure and prey availability. Similarly, there was no support for including demographic covariates such as killer whale population size (within or across pods). The number of males also did not appear to influence fecundity rates.

CONCLUSIONS

Our results provide strong evidence for reproductive senescence in killer whales, but more importantly, for a strong link between killer whale fecundity and the abundance of chinook salmon, a species that is susceptible to environmental variation and has high commercial value. Historically, killer whale growth rates may have been most affected by anthropogenic disturbance (live capture harvest), but the potential for future killer whale production may be limited by declines of chinook salmon. The fecundity for this population has increased slightly in recent years (Fig. 3). However, the increase appears to be primarily caused by a shifting age structure and concomitant recruitment of young females.

REFERENCES

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