

Quantifying the effects of prey abundance on killer whale reproduction

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Summary

1. Management decisions for threatened and endangered species require risks to be identified and prioritized, based on the degree to which they influence population dynamics. The potential for recovery of small populations at risk may be determined by multiple factors, including intrinsic population characteristics (inbreeding, sex ratios) and extrinsic variables (prey availability, disease, human disturbance). Using Bayesian statistical methods, the impact of each of these risk factors on demographic rates can be quantified and assigned probabilities to express uncertainty.

2. We assessed the impact of a wide range of factors on the fecundity of two threatened populations of killer whales *Orcinus orca*, specifically whether killer whale production is limited by availability of Chinook salmon *Oncorhynchus tshawytscha*. Additional variables included anthropogenic factors, climate variables, temporal effects, and population variables (population size, number of males, female age).

3. Our results indicate that killer whale fecundity is highly correlated with the abundance of Chinook salmon. For example, the probability of a female calving differed by 50% between years of low salmon abundance and high salmon abundance. Weak evidence exists for linking fecundity to other variables, such as sea surface temperature.

4. There was strong data support for reproductive senescence in female killer whales. This pattern of rapid maturity and gradual decline of fecundity with age commonly seen in terrestrial mammals has been documented in few marine mammal species. Maximum production for this species occurs between ages 20–22, and reproductive performance declines gradually to menopause over a period of 25 years.

5. Synthesis and applications. Our results provide strong evidence for reproductive senescence in killer whales, and more importantly, that killer whale fecundity is strongly tied to the abundance of Chinook salmon, a species that is susceptible to environmental variation and has high commercial value to fisheries. This strong predator–prey relationship highlights the importance of understanding which salmon populations overlap with killer whales seasonally and spatially, so that those salmon populations important as prey for killer whales can be identified and targeted for conservation efforts.

Key words: bayesian model selection, killer whale, management of endangered species, predator–prey interactions, resource limitation, salmon

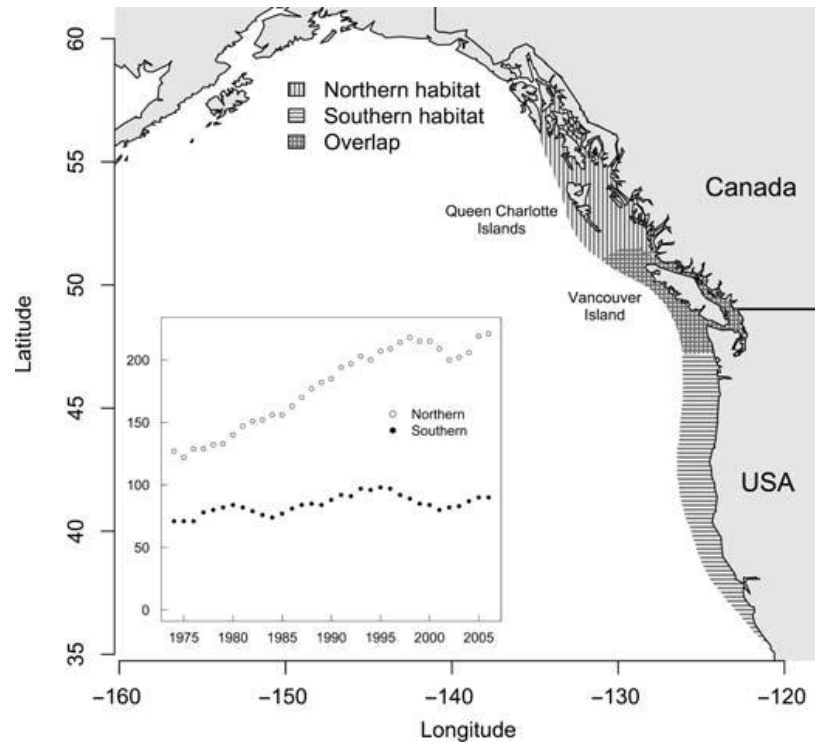
Introduction

Killer whales *Orcinus orca* are the most globally distributed cetacean species and are found in all of the world's oceans (Dalheim & Heyning 1999). Three ecotypes of killer whales are recognized within the species: mammal-eating 'transients', fish-eating 'residents', and the 'offshore' ecotype (Krahn *et al.* 2004). In the northeastern Pacific Ocean, long-term

data sets have been collected on two populations of fish-eating resident killer whales, found in inshore waters of Washington State and British Columbia. The larger Northern Resident population currently numbers approximately 220 individuals (Fig. 1). In some years, the range of Northern Residents may extend from southeast Alaska to Oregon (Fig. 1). This population has been slowly increasing in abundance since the 1970s, but in 2001 was listed as threatened under Canada's Species at Risk Act (SARA). As of 2008, the Southern Resident killer whale population consisted of 83 animals; this population

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Fig. 1. Habitat regions of Southern and Northern Resident killer whales (from Wiles 2004). The southern population is rarely seen north of Vancouver Island, while the northern population spends more time off the coast of Canada or southeast Alaska (north of Vancouver Island). Inset includes the historical population sizes for each population.



is found primarily in the southern part of the Georgia Basin waters during summer, and on the outer coast of Washington, Oregon and California in winter (Krahn *et al.* 2004; Olesiuk, Bigg & Ellis 1990). Southern Resident whales experienced declines in the late 1990s (when they were listed as endangered under SARA), and were listed under the US Endangered Species Act (ESA) in 2005, when the population dropped to 88 individuals.

In common with many cetacean species, killer whales are extremely long-lived, with some females thought to be 90 years old (Olesiuk *et al.* 1990). Reproductive maturity occurs by age 10 for most females, and previous studies have estimated that females produce calves approximately every 5.3 years over their reproductive life span (Olesiuk *et al.* 1990). Calves tend to be born in autumn and winter months, and they are first sighted during summer surveys. Each population of killer whales consists of pods (collections of matrilineal family units), and paternity often occurs across pods but not across populations (Barrett-Lennard 2000).

Existing data sets of Southern and Northern Resident killer whales are unique in their length and detail, providing one of the most detailed records of age-vs.-birth data for any mammal species. Since 1974, detailed records of individuals in each population have been collected using photo-identification techniques (Bigg *et al.* 1990). Data through 1987 were analysed by Olesiuk *et al.* (1990), who showed a decline in fecundity with age. In their analysis, few young animals with known ages were observed reproducing, and much of the data on the older females were based on approximate ages. With 20

years of additional data (1988 to 2007), we were able to more accurately establish the pattern of reproductive decline and senescence in these populations. In addition, we were able to compare the reproductive patterns in the Southern Residents, a population that has declined since the 1990s, vs. the Northern Residents, a population that has increased and may have levelled off recently (Fig. 1). These populations have similar diets and occupy partially overlapping geographic areas. However, they have been shown to be genetically distinct (Barrett-Lennard & Ellis 2001; Hoelzel, Dahlheim & Stern 1998). Although there is geographic overlap between the areas inhabited by these populations in some months (Fig. 1), Southern Residents may be more impacted by anthropogenic stressors, including whale watching, boat traffic (and associated vessel noise), and contaminants (Krahn *et al.* 2004; Wiles 2004). Fecundity in both populations may also be affected by demography; in the declining southern population, female fertility may be limited by the number of mature males, and in the northern population, fecundity may be affected by density dependence. Including both populations in a single model of fecundity reduces the chance of detecting spurious correlations, as each population has followed a unique trajectory (as the Southern Resident population has fluctuated, the Northern Resident population has followed an increasing trend).

In addition to comparing the pattern of age-specific reproduction between populations, we sought to understand how prey abundance might affect reproduction. Many of the prey populations targeted by these whales (salmon) are

themselves threatened or endangered, presenting a unique challenge for management. While the effect of prey density on fecundity has been shown in pinnipeds and terrestrial mammals (Caughley 1977; Fowler 1987; Roff 1992), there are reasons to suspect that prey availability might not affect fecundity in killer whales. Most studies that have found strong effects of prey limitation in pinnipeds have been during periods of extreme nutritional stress, such as during El Niño events (Huber 1991). As a long-lived species with the potential to store energy in blubber, female killer whales may be able to absorb the effects of normal year-to-year variation in prey levels. The ability to buffer the effects of years with low prey abundance has been shown in pinniped species (Boyd 2000); however, the degree to which killer whale reproduction might be affected by normal year-to-year variation remains unclear.

Materials and methods

Detailed age and birth data are available for killer whales because each whale has unique pigmentation in its saddle patch (the grey area located below the dorsal fin), and each individual has acquired permanent nicks, scratches, and scars on its dorsal fin (Bigg *et al.* 1990). The entire Southern Resident population has been censused annually by the Center for Whale Research (CWR) using photo-identification techniques. The Northern Resident population is surveyed annually by a variety of groups, including the Department of Fisheries and Oceans Canada, and due in part to the large population size, not all animals are seen each year. Photo-ID catalogues for both populations have been published and updated annually (Center for Whale Research 2007; Ford, Ellis & Balcomb 2000; Ellis, Ford & Towers 2007).

We focused on calf production or fecundity, where fecundity is defined as the product of the probability of giving birth and the probability of newborn survival to the first survey (Akçakaya 2000; Caswell 2001), because not all killer whale births are observed. Although reliable Southern Resident data have been collected by the CWR since 1976, only data since 1981 were included, because some covariate information for early years was incomplete. Over the years 1981–2007, a total of 159 mothers produced 299 calves; 50 Southern Resident females produced 80 calves and 109 Northern Resident females produced 219 calves (Supporting Information, Appendix S1). Years immediately before and after recorded births were omitted because it was impossible for females to have given birth in those years due to the length of the gestation and lactation period in killer whales.

PREY COVARIATES

The diet of Northern and Southern Resident whales is thought to be dominated by Chinook salmon, which is also the focus of major commercial and recreational fisheries in this region (Ford & Ellis 2006; Ford, Ellis & Olesiuk 2005). Fine-scale spatio-temporal data on the salmon biomass available to whales on a daily or weekly basis do not exist. As a proxy for the total annual salmon biomass available to whales, we used historical indices of abundance calculated by the Pacific Salmon Commission (PSC) and Pacific Fishery Management Council (PFMC). Although Chinook salmon are thought to be favoured prey items, we considered all available data representing Chinook and three other species of salmon over the range of southeast

Alaska to central California (Supporting Information, Appendix S2). Previous work has shown that PSC indices of Chinook have correlated with both killer whale survival and fecundity (Ford *et al.* 2005), and these PSC indices are thought to have the strongest correlation with ocean abundance (PSC 2008). Three PSC indices were included in our analysis – Chinook indices in southeast Alaska, northern British Columbia, and western Vancouver Island. As each index is composed of multiple stocks, we also used the stocks from each index to conduct a finer-scale examination of which stocks likely affect killer whale demography (Supporting Information, Appendix S2).

ENVIRONMENTAL COVARIATES

While ocean or environmental variables may not directly impact killer whales, environmental covariates may indirectly affect killer whales by impacting prey abundance (Mantua *et al.* 1997). To examine the effects of environmental covariates on killer whale fecundity, we considered a number of indices, including El Niño Southern Oscillation (ENSO; Schwing, Murphree & Green 2002), the Pacific Decadal Oscillation (PDO; Mantua *et al.* 1997), Northern Oscillation Index (NOI; Schwing *et al.* 2002), and localized sea surface temperature (Supporting Information, Fig. S6). These environmental variables may have differential impacts on various salmon life stages due to complicated anadromous life histories of salmon. Moreover, a time lag may exist between climate events and observed decreases in adult salmon abundance if the effect is strongest on early life stages (e.g. smolts).

DEMOGRAPHIC COVARIATES

The following time-varying demographic covariates were considered as predictors of fecundity to determine whether fecundity has responded to changes in the population structure:

1. The number of mature males one year prior to birth because fecundity in some pods may be limited by the number of males in the population (Krahn *et al.* 2004).
2. The number of males in the matriline, in the pod (but not matriline), and in other pods because the exact mating system is unknown.
3. The total number of animals, or number of mature males or females within a pod or matriline because fecundity may be affected by density dependence.
4. The number of previous births and years since the last birth because prior reproductive performance may impact later fecundity.

ANTHROPOGENIC EFFECTS

The population dynamics of Southern Resident killer whales may have been altered over the last 30 years as a result of increasing anthropogenic disturbances (Krahn *et al.* 2004). One anthropogenic risk factor that has been identified is the whale watch fleet, which increased nearly exponentially over the period 1975–2001 (Koski 2006). Other indices of anthropogenic impacts (recreational use and human population density, Supporting Information, Fig. S6) were also considered for the Southern Resident population.

Finally, we considered a set of temporal variables to account for the potential differences in anthropogenic impacts that may have changed over time, but which have not been monitored precisely (e.g. contaminants, other disturbances). It is unlikely that the changes in any of these covariates has been linear; we know, for instance, that levels of some contaminants are much higher than historical levels

(Krahn *et al.* 2007), but the magnitude of any changes remains unknown. To account for these differences, years were grouped as factor covariates. We considered groupings of years: (i) before and after 1987 (to determine whether a change has occurred since the analysis of Olesiuk *et al.* 1990), (ii) 5-, 7-, and 10-year periods following previous modelling work (Krahn *et al.* 2004), and (iii) 1977–1981, 1989–1992, and 2001–2003 because Foote *et al.* (2004) showed increasing levels of vessel noise between the periods.

TIME LAGS

Previous modelling efforts have suggested that a 1-year time lag should be used for all salmon covariates due to the 18-month gestation period of killer whales (Ford *et al.* 2005); we would expect the salmon available in the previous summer to be a better predictor of fecundity than salmon available in the year which the birth occurred if fecundity rates are positively correlated with prey density, and calves are primarily born in winter months. Arguments may also be made for alternative time lags; a time lag of 0 may be appropriate as many killer whale calves are not seen until they are several months old, and a time lag of 2 years may be appropriate if climate variables and salmon abundance affect fecundity. We considered alternative lags (0–2) for the majority of all demographic and external covariates to evaluate support for these hypotheses.

Statistical analysis

The response variable in our analysis – whether or not a female produced a calf – was modelled using binomial generalized linear models. In this framework, the response can be written as a non-linear function of covariates; $\log\{\text{Pr}(\text{birth})/[1 - \text{Pr}(\text{birth})]\} = XB$, where the logit-transformed probability of giving birth is a function of X (a matrix of covariates), and B (a vector of regression coefficients). Maternal age was modelled as a fourth order polynomial to allow the rate of maturity and rate of reproductive senescence to be asymmetric as was expected for a species with a long past-reproductive life span (Marsh & Kasuya 1986; Moss 2001). As a simple example, the logit of a model that includes age and an external variable (prey) as covariates for animal i at time t can be written as $XB = B_0 + B_1 \cdot \text{age}_{i,t} + B_2 \cdot \text{age}_{i,t}^2 + B_3 \cdot \text{age}_{i,t}^3 + B_4 \cdot \text{age}_{i,t}^4 + B_5 \cdot \text{prey}_t$. In this equation, the intercept and age-specific parameters determine the mean fecundity for all animals of a given age, and the prey coefficient represents a population effect, shared among all individuals.

One limitation of the above approach is that it does not account for heterogeneity among individuals, and it does not allow for variation in social structure. We developed two extensions to the fixed-effects model to separately include random effects either at the level of the individual or social unit (matriline). Modelling individual deviations with random effects is advantageous because it reduces the number of individual parameters that need to be estimated; rather than treating the number of individuals as a factor variable ($n - 1$ parameters), heterogeneity between individuals is determined by a global mean and standard deviation, $\delta_i \sim \text{Normal}(\mu_{\text{ind}}, \sigma_{\text{ind}})$. Regardless of how age or random effects were modelled, these data sets did not support the inclusion of additional

variation, either in individuals or matriline (Supporting Information, Appendix S3).

A large number of candidate models were constructed (in particular because of the number of time lags we considered). However, not all of the possible models were implemented (Supporting Information, Appendix S4). Parameter estimation was conducted using both Bayesian and maximum-likelihood methods. We examined the performance of Bayesian (Bayes factor, Kass & Raftery 1995) and likelihood (AIC, Burnham and Anderson 2002) model selection tools, as each has limitations (Link & Barker 2006; Ward 2008). Posterior probabilities and AIC model weights were calculated for each model as a measure of data support (Burnham & Anderson 2002), but these quantities were not used for model averaging because of potential biases they might introduce in predictions (Richards 2005).

Results

The Bayesian and maximum-likelihood estimation methods performed similarly. This was expected given the large amount of data and the simple logistic regression model used. The Bayesian approach favoured a model that included three covariates: female age (fourth order polynomial), Chinook salmon abundance near Vancouver Island, and a regional effect between the two populations (Table 1). AIC tends to favour slightly more complex models than other approaches, and thus, it is not unexpected that AIC favours a model that in addition to age and prey, also includes sea surface temperature. In both cases, the model that included the linear response of 1-year lagged Chinook abundance was more supported than higher order polynomials, or different lags (0 or 2 years, Supplementary Information, Table S1).

Female age appeared to be the dominant factor affecting fecundity in the best model (Fig. 2; Table 1). Maximum fecundity for both populations occurred between ages 20–22, and these rates are higher than previous estimates (Olesiuk *et al.* 1990). This concave pattern is similar to that seen in many other mammals (Caughley 1977), increasing relatively quickly (reaching 50% of the maximum at age 14) and declining slowly (declining to 50% of the maximum at age 39; Fig. 2). These ages are similar to those reported for another large dolphin species (pilot whales *Globicephala macrorhynchus* reach 50% at ages 8 and 33; Marsh & Kasuya 1986), but killer whale ages are slightly larger (as is life expectancy). After age 39, reproductive performance declines sharply – a trend also observed in other species (e.g. Paul, Kuester & Podzuweit 1993).

We were able to show that Chinook abundance affects yearly fecundity rates at the population level (calves/female) by controlling for the effect of age. More specifically, the index of Chinook salmon abundance available to fisheries off the West Coast of Vancouver Island in the previous year was positively correlated with fecundity (Table 1). Following highly productive salmon years, the probability of calving is 50% higher at the population level compared to years following low salmon years (Fig. 3). Although studies of terrestrial

Table 1. Parameter estimates (Bayesian posterior modes) for the three models of killer whale reproduction most supported by the data (Supporting Information, Tables S1–S2 include additional models). CVs are given in parentheses, and are identical to the maximum-likelihood CVs. Four age terms are included, representing the fourth order polynomial. External covariates included are Chinook salmon abundance off the West Coast of Vancouver Island (includes numerous migratory stocks), the difference between the populations (region effect), and sea surface temperature. Bayes factors slightly favour model 2, while AIC favours model 3; together these three models represent more than 66% of the posterior probability and AIC weights

Parameter	Model 1	Model 2	Model 3
Intercept	-24.01 (0.17)	-23.70 (0.17)	-21.91 (0.18)
Region (southern)		-0.253 (0.57)	-0.256 (0.57)
Age	3.65 (0.20)	3.60 (0.20)	3.61 (0.20)
Age ²	-0.216 (0.22)	-0.214 (0.22)	-0.214 (0.22)
Age ³	0.00545 (0.24)	0.00539 (0.24)	0.00541 (0.24)
Age ⁴	-0.0000499 (0.26)	-0.0000494 (0.26)	-0.0000496 (0.26)
Vancouver Island Chinook	0.991 (0.28)	0.999 (0.28)	0.880 (0.28)
Sea surface temperature			-0.201 (0.59)
Posterior probability	0.25	0.30	0.13
AIC weight	0.14	0.24	0.36

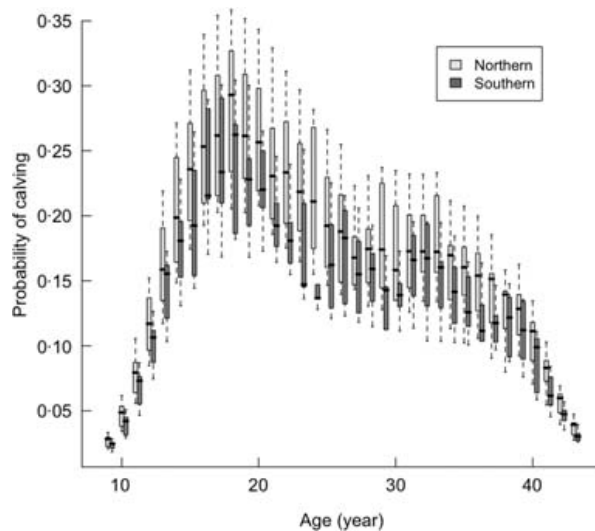


Fig. 2. The estimated effect of age on the probability of calving (estimated from the Bayesian version of Model 2, Table 1). The boxes represent the first and third quartiles around the median, and the whiskers represent the range of the variation.

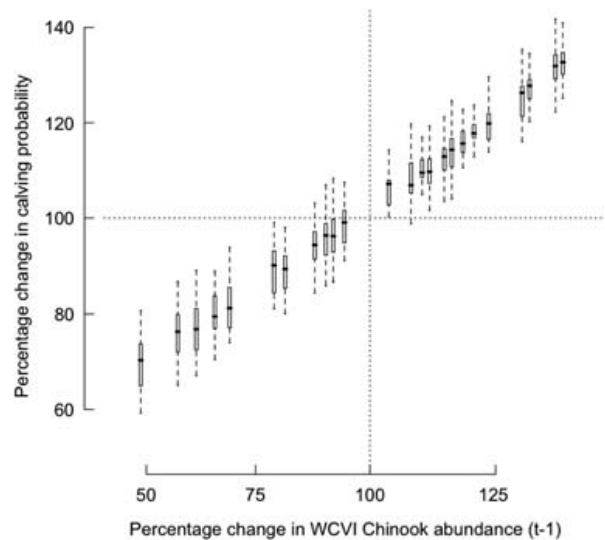


Fig. 3. Percentage deviation from the model predicted calving probability (using the Bayesian version of Model 2, Table 1) as a function of the percentage deviation in Chinook abundance relative to the 1980–2006 mean. Deviations for each variable are calculated as deviations from mean, x_i/\bar{x} while the y-axis is calculated from model predictions, the x-axis is calculated from the PSC indices.

mammals have shown that the age at maturity is the parameter most sensitive to prey limitation (Eberhardt 2002), we were not able to detect any change in the age of maturity of either population – detecting changes in age at maturity of extremely long-lived species may require much longer time series of data. Our sample of animals reaching maturity is small and the generation time is relatively large (> 20 years) relative to other vertebrate species that have shown rapid changes in age at maturity.

There is weak evidence for including an additive main effect allowing for a regional difference between populations (Pr = 66%, Supporting Information, Table S1), and if included, this effect is small (Table 1). The Northern and Southern Residents have some degree of overlap in their habitat (Fig. 1), and while they may share the same prey species (Ford *et al.* 2005),

it is unclear whether the populations share the same prey populations. Inclusion of the regional effect translates into the southern population having slightly lower calving rates relative to their northern counterparts (Table 1, Fig. 2). Although none of the predictor variables we considered appeared to be responsible for a difference between these populations, one factor that needs to be studied further is the effect of toxins. The Southern Residents are known to carry higher contaminant loads (Krahn *et al.* 2004). Accumulation of some contaminants over a life span may decrease reproductive performance (Ross *et al.* 2000). It remains unclear what effects contaminants have on killer whale fecundity

because appropriate contaminant data do not exist and the bioaccumulation process remains unknown.

After accounting for salmon abundance, there appeared to be no support for additional temporal effects, regardless of whether year was treated as a numeric variable or groups of years were treated as factor variables. Killer whale fecundity, therefore, does not appear to have been affected by variables other than age structure or prey availability. Similarly, there was no support for including demographic covariates such as killer whale population size (within or across pods). The lack of support for density-dependence in realized killer whale fecundity may be because both populations are well below their historical population sizes (Olesiuk *et al.* 1990). The number of males did not appear to influence fecundity rates, suggesting that these populations are not affected by mate limitation.

Although salmon abundance is known to be affected by climate variability, and killer whale fecundity is correlated with indices of Chinook salmon, it may be surprising that none of the climate variables considered – either localized processes such as sea surface temperature, or regional forcing patterns such as ENSO or PDO – appeared to impact killer whale fecundity (Table 1; Supporting Information, Table S1). This result held for all time lags considered. The lack of support for climate variation may be due to the complex life history of Chinook salmon. Factors such as sea surface temperature probably affect Chinook salmon over most of their lives, but are thought to have the highest impact during juvenile life stages, when salmon leave freshwater for the marine environment (e.g. high PDO typically results in above-average stream flows, having a positive impact on juvenile survival; Mantua *et al.* 1997). Further, annual abundance estimates of returning Chinook represent a mix of brood years (individuals aged 2–6), each brood being affected differently by climate signals because of different years of ocean entry (Scheuerell & Williams 2005). A more realistic model might consider each climate variable across a mixture of time lags. However, parameterizing a model with existing Chinook salmon data is not possible because detailed age compositions of each population are not collected every year.

We generated a large number of simulated killer whale female cohorts, each approximately the same size as the number of mature females in the Southern Resident population, to fully understand the management implications of how a decline in Chinook salmon abundance affects killer whale growth and viability. Each cohort experienced consistently poor, average, or high salmon abundance, and was subjected to demographic stochasticity (Supporting Information, Appendix S5). The number of females produced by each cohort was recorded over the simulations, and used as a measure of population growth (Fig. 4). When WCVI Chinook salmon abundance is equal to the 1980–2006 mean, killer whale population growth remains positive in > 99% of all simulations. Simulated female cohorts that experience salmon abundance that is 50% of average (similar to the levels observed in 1995–1996) may experience positive growth, but also have a 15% chance of declining (this decline may become even greater when survival is considered).

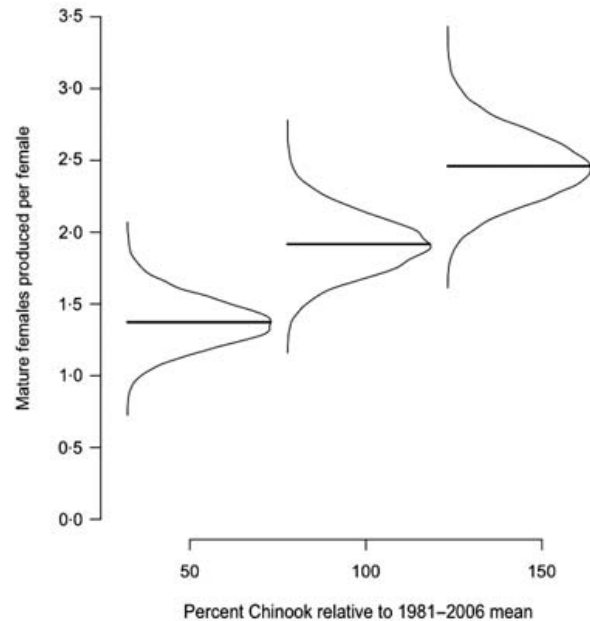


Fig. 4. Relationship between the 1-year lagged PSC salmon abundance index and killer whale growth rate (production of females per female).

Discussion

Although previously published work on killer whale fecundity has shown evidence of reproductive senescence (Olesiuk *et al.* 1990), our analysis is the first to show that killer whale reproduction follows the rapid increase in fecundity and convex fecundity curve seen in other mammals (Packer, Tatar & Collins 1998). Age-specific fecundity of these populations is characterized by a rapid increase in fecundity starting around age 10, reaching a maximum between ages 20–22, followed by a slow decline to age 40, and then a rapid decline to full reproductive cessation (Fig. 2). This general pattern of early improvement and subsequent decline in fecundity of killer whales is consistent with the patterns observed in other mammals, including roe deer *Capreolus capreolus* (Hewison & Gaillard 2001), elephants *Loxodonta africana* (Moss 2001), grey seals *Halichoerus grypus* (Bowen *et al.* 2006), and fur seals *Arctocephalus gazella* (Lunn, Boyd & Croxall 1994). Also our finding that reproduction declined gradually between the ages of 23 and 40 is consistent with theoretical work on the evolution of senescence which predicts that in long-lived species with low adult mortality, like killer whales, there should be selection for reproductive success later in life (Hamilton 1966; Williams 1957). Studies on pinnipeds have found direct trade-offs between female survival and reproduction, presumably due to a trade-off between energy for maintenance vs. energy for reproduction (Boyd *et al.* 1995). Such a trade-off may play a role in the killer whale reproduction. We did not find evidence for this in killer whales; however, too few females have died to estimate this relationship with much statistical power.

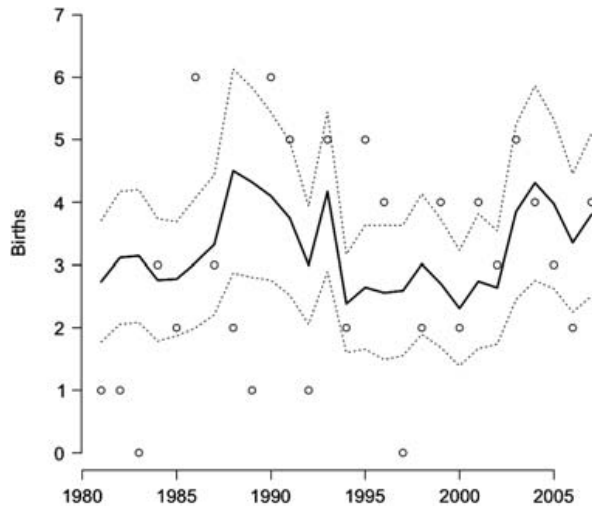


Fig. 5. Model predicted annual fecundity (Model 2, Table 1) for the Southern Resident killer whales (solid line) along with the observed number of calves (points); dashed lines represent 2 standard errors.

Although the Southern Resident killer whale population has been listed under both SARA and ESA, it appears that the estimated fecundity for this population has increased slightly in recent years (Fig. 5). The increase in expected births is primarily caused by a shifting age structure, and recruitment of more young females. The reason for the difference in birth rate between the 1980s and the most recent decade is that between 1964 and 1974, the Southern Resident population was the target of live capture harvests for the aquarium trade that ultimately removed at least 34 animals from the population; the expected fecundity in the 1980s would have been substantially higher had these animals not been removed – of the harvested individuals, a minimum of 13 were females (Olesiuk *et al.* 1990). As the potential for rapid growth in this species is low, it is important for managers to consider the reproductive value of each member of the population; while two hypothetical females (ages 22, 45) contribute equally to recovery goal metrics, such as total population size, there are considerable differences in their expected future reproductive output.

Life-history evolutionary theory suggests that reproductive effort should be allocated to periods with favourable breeding conditions for organisms inhabiting variable environments (Roff 1992). The relationship between prey density and fecundity has been previously shown in pinnipeds and terrestrial mammals (Caughley 1977; Fowler 1987), but this analysis is the first mammalian study we are aware of to estimate the strength of the relationship between prey abundance and the probability of calving, while simultaneously accounting for reproductive senescence and age structure (Fig. 3). In years when prey density is low, killer whales may expand their summer ranges (Hauser *et al.* 2007) and may have less cohesive social groups (C. Emmons, K. Parsons, NOAA, personal communication). Increased search time and less social

interaction are mechanisms that may directly affect reproduction. In common with many indices of Pacific salmon, the index of Chinook developed by the PSC is somewhat cyclic – following a low period during 1996–2001, the index peaked in 2004, and recently appears to be declining, suggesting that if the pattern continues, fecundity rates could drop to lower-than-average levels over the next 5 years. One potential stressor not explored in this analysis is the cost of foraging over large spatial scales. In recent years, sightings of some killer whale pods included in this analysis in Monterey have coincided with large Chinook salmon runs (Wiles 2004). It is unclear whether these migrations are a new phenomenon, and what effect they have on killer whale demographic rates because historic data on killer whale movements are sparse.

The WCVI Chinook abundance index is dominated by salmon from Puget Sound, and the Columbia and Fraser rivers. This fishery has been managed under a target exploitation rate policy, and since 1999, the estimated catch for the troll and recreational fisheries has been 13% below the target catch (PSC 2008). In recent years, the fishery also has enacted temporary closures when abundance is less than expected. For example, the fishery responded with closures in some summer months when the WCVI abundance index fell in 2006 and 2007 (to < 80% of the 1979–2006 mean). We considered each of the stocks in the WCVI fishery as covariates in our models to identify which particular Chinook stocks were most likely to be tied to killer whale demography, and we found that one of the most abundant Chinook stocks was strongly supported over others (late-run Fraser River, Supporting Information, Table S2). The importance of Fraser River Chinook is consistent with current hypotheses about prey composition (Ford & Ellis 2006) and results from genetic stock identification (although these results suggest a large contribution from early run Fraser Chinook; M. Ford, NOAA, personal communication). Although catch for the WCVI fishery has been below target, the escapement goals for the late-run Fraser indicator stock (Harrison River) have not been reached in recent years (52–68% in 2006; PSC 2008).

We would expect WCVI abundance to decline for several more years, possibly below 50% of the long-term mean if recent patterns in Chinook abundance follow the same pattern observed during the 1990s. If this occurs, there is likely to be a noticeable negative effect on killer whale reproduction, and it will become important for managers to consider the effects of fishery harvest rates and escapement goals on the abundance of Chinook available as prey for whales (NMFS 2007). The late-run Fraser River Chinook stock is important to both US and Canadian fisheries; over the period 1985–2005, this single stock represented the largest proportion of catch in three PSC-monitored fisheries (Central British Columbia, WCVI, Strait of Georgia), and contributed the second largest proportion in a fourth (Washington and Oregon States). Further, it will become important to predict annual seasonal prey requirements for killer whales as more data are collected on killer whale habitat use. Over the course of a year, salmon stocks are affected differently by fisheries, and the significance of individual stocks contributing to killer whale diet changes

over a season (e.g. early-run Fraser being more important in May–June, late-run Fraser being more important August–September). The importance of each salmon stock also changes on a larger scale; each population has unique year-specific characteristics, such as age distribution and run-timing that affect total abundance, and salmon available to fisheries and whales.

Although the estimated regional difference in fecundity rates between Northern and Southern Residents was found to be small and associated with considerable uncertainty (Table 1), this difference provides an indication that the production of Southern Resident killer whales might not be as high as it could be. Based on how data are collected, the true difference in fecundity between the two populations is likely greater than our estimated difference. As some individuals from the northern population are not seen in each year, there is a chance of surveys missing newborn calves that do not survive to age 1. An alternative explanation for the difference between these two populations is simply that the southern population may be a victim of chance. Small, closed populations, such as both of the killer whale populations in our analysis are more prone to the effects of demographic stochasticity, and have been shown to have significantly decreased heterozygosity and elevated extinction risk (Paetkau *et al.* 1997; Lande 1988; Barrett-Lennard 2000).

While our analysis confirms evidence for a correlation between predator production and availability of prey density on an annual time-scale, the predator–prey relationship needs to be better understood at finer time-scales. Although somewhat intuitive, better management advice will occur after crucial data gaps are filled (specifically, fine-scale nutritional requirements and habitat use by predators and prey). Estimates of bioenergetic requirements for killer whales are being developed based on captive studies (D. Noren, NOAA, personal communication), but several questions remain. (i) What is the length of time that these apex predators can tolerate without food? (ii) To what degree does prey quality (e.g. contaminants) affect nutrition and reproduction? Understanding overlap in habitat use by predators and prey is also crucial. For any predator population that exhibits seasonal movement or migration, the dietary importance of individual prey populations changes over time; fine-scale spatial data will allow managers to prioritize which Chinook salmon populations must be protected for killer whale recovery.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Description of killer whale data

Appendix S2. Description of salmon data

Appendix S3. Modelling individual variation in fecundity

Appendix S4. Model selection

Appendix S5. Description of simulations

Fig. S1. Distribution of female ages.

Fig. S2. PSC Chinook salmon indices.

Fig. S3. Individual stocks from the PSC indices.

Fig. S4. Observed ages of reproductive females over time.

Fig. S5. Predicted fecundity rate for a fecundity model that is not biologically plausible.

Fig. S6. Climate and anthropogenic covariates.

Table S1. Comparison of models using different time lags and covariates

Table S2. Comparison of models using Chinook indices at the stock level

Table S3. Correlations between environmental covariates

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