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2014 Update of Southern Resident Killer Whale Demography

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Background

During the annual summer census, the Center for Whale Research reported that 2 animals have likely died over the last calendar year, leaving the SRKW population at 78 animals. Since the bilateral workshops in 2011-2012, the population has continued to decline from 87 (2 births, 11 deaths). This document provides an update of demographic rates and population dynamics since 2010.

Calculating lambda

Following the exact methodology described in Ward et al. (2013), the updated census numbers were used to calculate estimates of λ . Recall that λ represents the population growth rate at equilibrium (Caswell 2001), and is generally based only on the survival and reproduction of females. In addition to updating λ , we were also interested in comparing the updated λ to that presented in Ward et al. (2013). The updated posterior distribution of λ is shown below (Figure 0.1). Compared to the previous estimate (which used data including the 2011 census), the posterior distribution of λ is more negative (Figure 0.1).

Why is lambda still positive?

An obvious question in examining the estimate of λ is why the estimate is not centered more closely on 1.0 (corresponding to zero population growth). The limitations of using λ to quantify population growth are discussed in λ , but this apparent discrepancy is rooted in the fact that λ is only affected by deaths of females who are of reproductive age, or younger. Looking at the age and sex distribution of females who have gone missing over the last 3 years, the majority of these animals are either males or older females.

	Died	Sex	Age
J8	2013	F	80
K40	2012	F	49
L2	2012	F	52
L5	2012	F	47
L12	2012	F	78
L26	2013	F	56
L78	2012	М	33
L79	2013	М	34
L100	2014	М	13
L112	2012	F	3
L53	2013	F	36

Another reason why λ has remained slightly greater than 1 is that the total number of reproductive females recruited to the population has increased

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Fig. 0.1. Updated posterior distribution of lambda for the Southern Resident killer whale population, 1979-2014. The histogram represents the most recent estimate using data through summer 2014, and the solid line represents the estimate using data through summer 2011.

over time. In other words, at the start of the study, there were 25 females of reproductive age, but since the early 1980s, this number has fluctuated between 28-33 (currently 31, see also Ward et al. 2013).

Declines in post-reproductive females

With these recent deaths, there are now only 3 post-reproductive females in the SRKW population: J2, L25 (c. 86), and L27 (49). The oldest males in the SRKW population are now L41 (37) and K21 (28). Another way of illustrating these changes in the population are to plot the total number of post-reproductive females (> 43 years old) over time, which shows a declining trend since the start of the study (Figure 0.2). The mechanism responsible for this decline, or the presence of a high proportion of older animals in the late 1970s is unclear. The majority of animals harvested for aquaria during the 1960s and 1970s were < 10 years old. This reduction would have had the effect of both (1) immediately reducing any density dependent effects and (2) skewing the age structure toward older animals. The presence of these older animals may also be in part due to social or cultural reasons - however, other populations of resident killer whales in the Northeast Pacific have a much smaller proportion of these older females.



Fig. 0.2. Post-reproductive females (> 43 years old) in the SRKW population.

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Changing age structure

The decline in post-reproductive SRKW females is relevant to examining shifts in the age composition of the SRKW population over time, as well as how the current age structure compares to recovery goals. One of the recovery targets in the SRKW recovery plan was acheiving an age structure more similar to that of Northern Resident killer whales, which was 47% juveniles, 24% reproductive females, 11% post-reproductive females, and 18% adult males (Olesiuk et al. 2005; NMFS 2008). The age composition of NRKW has shown a steady increase in the number of females (both reproductive and post-reproductive), while the number of males has remained essentially constant (Figure 0.3). In contrast, the number of males in the SRKW population has increased slowly (Figure 0.4).

Changes in fecundity

One potential area of concern for SRKW viability is that no viable calves were produced in 2013, and none have been produced to date in 2014. 2013 or 2014 were not the first year with zero calves (Figure 0.5), however this is the first 2-year span when no SRKW calves have been born since the CWR survey started in the late 1970s. Using the logistic model of fecundity as a function of age (Ward et al. 2013) we can calculate the expected number of births in 2014, given the current age structure of the SRKW population (Figure 0.6). Because of the small sample sizes associated with the SRKW population, and no covariates (like Chinook salmon) are included in this simple analysis, there is high uncertainty in these predictions.

Unproductive females

There are many reasons why calves may not be being born. Factors include lack of prey, mate limitation (in particular, if pods don't spend lots of time together), potential impacts of contaminants, diseases, or genetic inbreeding. Several females are currently in their prime reproductive ages (early 20s; Ward et al. 2009). The distribution of females that are reproductive aged or younger is as follows (number of viable calves produced in parentheses):

J pod	Age	K pod	Age	L pod	Age
J14(6)	40	K13(4)	42	L47(7)	40
J16(5)	42	K14(5)	37	L54(3)	37
J17(3)	37	K16(2)	29	L55(5)	37
J19(2)	35	K20(1)	28	L72(1)	28
J22(2)	29	K22(2)	27	L77(2)	27
J28(2)	21	K27(1)	20	L82(1)	24
J31	19	K42	6	L83(1)	24



NRKW 1979-2010

Fig. 0.3. Age composition of Northern Resident killer whales, 1979-2010. Only data used through the bilateral workshops has been included, and stages are identical to those presented in Ward et al. (2013). Females are broken into reproductive females ("Female1") and post-reproductive females ("Female2"), and males are broken into young ("Male1") and old ("Male2").

J32	18	K43	4	L86(2)	23
J35(1)	16			L90	21
J36	15			L91	19
J37(1)	13			L94(1)	19
J40	10			L103	11
J41	9			L113	5
J42	7			L118	3
J46	5			L119	2
J47	4				



Fig. 0.4. Age composition of Southern Resident killer whales, 1979-2010. Data through the summer 2014 census has been included, and stages are identical to those presented in Ward et al. (2013). Females are broken into reproductive females ("Female1") and post-reproductive females ("Female2"), and males are broken into young ("Male1") and old ("Male2").

Because estimating the effects of age (4th order polynomial, Ward et al. 2013) and external covariates (e.g. salmon) can be complicated, we simplified the analysis by focusing on all births by SRKW females between the ages of 21-27. Assuming relative births by these females to be invariant to age (this is near the window of peak reproduction; Ward et al. 2009), we concentrated on estimating the time effect (linear in link-space). In both frequentist and Bayesian statistics, this trend was estimated to be negative (Pr < 0 - 98.4%). In terms of the effect size, the probability of an animal from this age range giving birth changed from - 30.5% in 1980 to 7.4% in 2014.



Fig. 0.5. Number of SRKW births per year.

Trends in the sex ratio at birth

During the bilateral workshops, a comparison between NRKW and SRKW sex ratios at birth was presented, with calves being approximately 55% female in the NRKW population and 45% female in the SRKW population. This difference was assumed to be due to chance, and there was no evidence for a significant trend. As the proportion of males in the SRKW population has increased over time (Figure 0.4), it is worth re-examining the evidence supporting any trend. To do this, we fit maximum likelihood and Bayesian GLMs (equivalent to logistic regression), for SRKW births over the period 1977-2014. In a maximum likelihood framework, the coefficient for the year effect is not statistically significant (p > 0.25), and its inclusion is not supported by model selection (increases AIC by 0.46). Another way to quantify the uncertainty in



Fig. 0.6. Estimated number of SRKW births in 2014.

this effect is to use output from the Bayesian GLM to quantify the probability that there has been a positive trend in sex ratio at birth (with births becoming more male). This analysis highlights that the probability of a positive trend is approximately 90% (Figure 0.7).

Estimating Carrying Capacity

As discussed in Ward et al. (2013), there are a number of approaches for estimating carrying capacity and density dependence in SRKW. Ecosystem based approaches to this problem are ongoing, and will be addressed between Fall 2014 - Fall 2016. Simpler estimates of carrying capacity (the same as presented by Ward et al. 2013) rely on fitting univariate models to time series



Fig. 0.7. Estimated change in the sex ratio at birth, shown with raw data (top) and the posterior distribution of the coefficient related to the year effect (bottom). The probability that there has been a positive trend in the sex ratio at birth (becoming more male) is just over 90%.

of total abundance data for a population. We fit a Gompertz state-space model to the time series of SRKW counts, incorporating the last 3 years of data. This model can be described as

$$x_t = bx_{t-1} + u + \delta_t \tag{0.1}$$

where x_t represents the log-abundance at time t, b represents a density dependent parameter, u represents the trend or level parameter, and the process deviations representing environmental stochasticity are normally distributed,

$$\delta_t \sim Normal(0, \sigma) \tag{0.2}$$

The second component of the Gompertz state-space model involves linking the latent process model to observed counts. This observation equation describes measurement error,

$$y_t = x_t + \varepsilon_t \tag{0.3}$$

where the observation error is also assumed to be normally distributed,

$$\boldsymbol{\varepsilon}_t \sim Normal(0, \boldsymbol{\gamma})$$
 (0.4)

We estimated all parameters of the model in a Bayesian framework. Rather than estimate b directly, we treated it as a derived parameter, because band u control carrying capacity, K = u/(1-b). We placed a uniform prior on K from 70-150. Unlike in the bilateral workshops, when this procedure resuled in a bimodal parameter estimate, the estimated posterior for K is more unimodal, centered near 85 animals (Figure 0.8). Previous reports have suggested a higher range of carrying capacity in the 1970s. For example in the SRKW recovery plan, an estimate of 129 was used (estimated population size of 79 animals in 1979 + 47-48 removals over 1962-1973) (NMFS 2008, Hoyt 1984). This estimate may be slightly high, but a simple population model can be constructed to show that carrying capacity (K) would have probably been >110 animals, to achieve a population size of 79 animals in 1979 (this assumes maximum growth rate, 'Rmax' = 4% and density dependence is linear). R code that can be used to explore this more is below. One of the other critical assumptions of this model is that carrying capacity has been constant through time; because carrying capacity for apex predators is driven by abiotic and biotic factors lower in the food web, it's possible carrying capacity has declined over time. Over the next several years, we will continue to explore how carrying capacity has changed, and how this influences tradeoffs (Figure 0.9).



Fig. 0.8. Estimated posterior distribution of SRKW carrying capacity from the univariate Gompertz state space population model, using data from 1979-2014.

Summary

Supplementary Tables and Figures



Radar plot of NE Pacific food web by decade, 1970-2010

Fig. 0.9. Radar plot by decade, showing some of the tradeoffs we're exploring in a food web model of the NE Pacific.