Running Head: Killer whale condition and survivorship

Full Title: Survival of the Fattest: Linking body condition to prey availability and survivorship of killer whales

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#### Abstract

Recovering small, endangered populations is challenging, especially if the drivers of declines are not well understood. While infrequent births and deaths may be important to the outlook of endangered populations, small sample sizes confound studies seeking the mechanisms underlying demographic fluctuations. Individual metrics of health, such as nutritive condition, can provide a rich data source on population status and may translate into population trends. We use aerial photogrammetry data to build a Bayesian predictive model of body condition changes in endangered Southern Resident killer whales (SRKWs), providing a unique test case comprising decades of demographic monitoring, a small population size, and repeated condition measurements of individual whales. We demonstrate that fluctuations in SRKW body condition can be explained by the abundance of Chinook salmon, providing targeted management opportunities. We also show that whales in poor body condition-reflecting depleted fat reserves-are more likely to die, linking changes in condition to population viability.


Key words: Orcinus orca; resident killer whale; foraging ecology; body condition; drones; photogrammetry; adaptive management; multi-state modeling.

## Introduction

Endangered species with small population sizes approaching extinction or local extirpation present a diversity of management challenges (Soulé 1987, Dennis 1989). When the causes of population declines are not well established it is difficult to identify management strategies that will prevent declines and promote recovery. Studies of small populations by definition suffer from sample size limitations (Walsh 2000, Brosi and Biber 2009), complicating efforts to identify stressors that may be influencing population trends (Schönbrodt and Perugini 2013). For example, infrequent births or deaths may have dramatic impacts on population trends, but may be too sparse to identify mechanisms. In these cases, non-invasive metrics of individual health can help identify drivers of population trends and allow for management strategies that preempt demographic casualties that impact population viability, such as the loss of reproductive females.

Nutritive condition in long-lived vertebrates can provide a sensitive signal of short-term individual or population health. Changes in condition may reflect changes in the environment or foraging success, and persistent variation may translate into population trends (Berger 2012, Boulanger et al. 2013, Vindenes et al. 2014). Aerial imaging technology has provided one example of such non-invasive individual health metrics (Perryman and Lynn 2002). Photogrammetry with remotely controlled drones has been used increasingly over the past 5-10 years as drones have become cheaper, safer and more efficient compared with traditional photogrammetry using manned aircraft (Durban et al. 2015). These methods have been widely applied to both terrestrial and marine species (Perryman et al. 2014, Hu et al. 2020). Working with marine or other aquatic organisms is particularly challenging, as individuals are highly mobile and may spend little time near the surface where they can be imaged. Nevertheless, aerial
photogrammetry has been used to collect individual measurements of marine mammal species including investigations of life history characteristics (Christiansen et al. 2016, Groskreutz et al. 2019) and nutritive condition (Christiansen et al. 2018, Fearnbach et al. 2018, 2019). A strength of aerial photogrammetry is that it can non-invasively provide quantitative metrics of body condition at the individual level (Durban et al. 2015, Fearnbach et al. 2018), which can be used to evaluate the health or status of a large portion of a population in near real time. Demographic trend data, in contrast, has high inherent variability in small populations and may need to be collected for years before it provides reliable inferences about population health.

Collecting individual health data from wild populations may be challenging, particularly if individuals can't be identified or the population is not censused. Killer whales (Orcinus orca) represent an ideal case for relating individual health metrics to the environment, as population sizes are typically small, and individuals are readily identifiable. One of the smallest populations of killer whales, the Southern Resident killer whale (SRKW) population, is censused annually and demographic characteristics (age, sex) have been recorded for the entire population since the mid 1970s (Center for Whale Research 2020). This small ( $\mathrm{n}=73$ ) population of fish-eating killer whales is found in the eastern north Pacific (Ford et al. 1998) with a range including coastal waters from central California to Southeastern Alaska, and core summer habitat in the Salish Sea between Puget Sound and Southern Vancouver Island (National Marine Fisheries Service 2019). Because of its small size and a decline in abundance of approximately $25 \%$ since 1995 , the SRKW population is listed as endangered under the Endangered Species Act (ESA) in the United States and the Species-at-Risk Act (SARA) in Canada. The diet of SRKWs comprises primarily Chinook salmon (Oncorhynchus tshawytscha), although other species such as coho salmon
(Oncorhynchus kisutch), chum salmon (Oncorhynchus keta), halibut (Hippoglossus stenolepis) and groundfish have also been identified in their diets (Hanson et al. 2010, Ford et al. 2016). Three main stressors are thought to be responsible for SRKW population declines: 1) elevated levels of environmental pollutants in their core habitat range that could impact survivorship and reproductive success (Krahn et al. 2009); 2) increasing vessel noise and disturbance in the Salish Sea which could interfere with communication and foraging efficiency (Lusseau et al. 2009); and 3) declining Chinook salmon populations and therefore prey scarcity (Ford et al. 2010), which in addition to direct effects could compound the other stressors.

Several studies have supported the hypothesis that prey limitation is a primary threat to the SRKW population, linking aggregates of Chinook salmon abundance to both fecundity and mortality (Ward et al. 2009, Ford et al. 2010, Vélez-Espino et al. 2014) as well as to declines in adult body size (Fearnbach et al. 2011, Groskreutz et al. 2019). However, the range of both SRKWs and their salmon prey is enormous, encompassing over $3,000 \mathrm{~km}$ of coastline, and identifying the prey populations that are most important for SRKWs is challenging. Chinook salmon face a complex suite of stressors including habitat modification and degradation (Greene and Beechie 2004), restricted access to spawning tributaries (Sheer and Steel 2006), fisheries pressure (Ruckelshaus et al. 2002), increased natural mortality due to recovering marine mammal populations (Chasco et al. 2017), and climate impacts (Crozier et al. 2008). Chinook populations from four tributaries within the SRKW range are themselves listed as endangered in the United States or Canada, with several others listed as threatened. To date, no studies have been able to identify relationships between specific salmon populations and SRKW survivorship or population health (Pacific Fishery Management Council 2020).

Aerial photogrammetry can provide a precise measure of individual killer whales' nutritive condition by quantifying the relative amount of adipose fat stored behind the cranium; as individuals decline in nutritive condition, they metabolize adipose fat in addition to blubber stores (Fearnbach et al. 2019). As such, photogrammetry datasets potentially provide more power to evaluate relationships between prey abundance and population status compared with efforts to link prey to infrequent births and deaths. In this study, we used aerial photogrammetry images of individually-recognizable SRKWs collected in 7 September field efforts across 12 years (2008-2019) to evaluate how changes in body condition might be related to the abundance of different Chinook salmon populations. The SRKW population is composed of three distinct collections of matrilineal family units (hereafter referred to as J , K and L pods) (Parsons et al. 2009) and we considered each pod separately in our analyses based on previously described differences in range and movement patterns (Riera et al. 2019, National Marine Fisheries Service 2019).

## Methods

## Data collection

Aerial images of Southern Resident killer whales were collected in the Salish Sea near the San Juan Islands, WA (Fearnbach et al. 2011, Groskreutz et al. 2019) in the month of September in each of seven years. Images were collected from a manned helicopter in 2008 and 2013 (Fearnbach et al. 2011, 2018) and using a drone in 2015-2019 (Durban et al. 2015, Fearnbach et al. 2019). Briefly, vertical images were collected using a digital camera at altitudes of 230-460 m by helicopter and 25-45 m by drone. Despite changes in aircraft platforms, all images were
obtained with a Normal lens to ensure a flat image with no wide-angle distortion, with the specific camera and lens chosen based on aircraft altitude to achieve a water-level pixel resolution of $1-2 \mathrm{~cm}$ (Durban et al. 2015). Research activities were permitted by the National Marine Fisheries service in the U.S. and the Department of Fisheries and Oceans in Canada, and aerial photogrammetry was approved as an observational (non-invasive) method by the Institution Animal Care and Use Committee of the NOAA Southwest Fisheries Science Center Marine Mammal and Turtle Division. Individual whales can be identified by unique markings that are visible from aerial images, allowing measurements to be linked to individual whales of known age and sex (Fearnbach et al. 2011, 2019, Durban et al. 2015). As a quantitative metric of body condition we used the eye patch ratio (EPR), which is the ratio of the pixel distance between the inside of the white eye patch pigmentation at their anterior end relative to their distance at $75 \%$ of the eye patch length, described in Fearnbach et al. (2019) (Figure 1). The eye patch ratio is a sensitive metric of nutritive condition as it measures the relative amount of adipose fat stored behind the cranium. As killer whales become nutritionally stressed, they lose this adipose tissue along with blubber fat reserves, resulting in lower EPRs, and as such this is a more sensitive metric of nutritive condition in killer whales compared to other commonly used metrics such as head width to body length ratios (Fearnbach et al. 2019). Multiple measurementquality images were available of a single whale on a given day and within years, and we used the mean EPR for each whale in each year because EPR calculations had very low variability (e.g. typical coefficients of variation of 0.003 to 0.008 for within year variability of a given whale) (Fearnbach et al. 2019).

Accounting for age \& sex

To prepare the raw eye patch ratio data for analysis, we first fit a generalized additive model to the EPRs using the mgcv package (Wood 2006) in R (R Core Team 2016) to account for expected variability in nutritive condition and EPRs by age and sex. Age and sex data were available from long-term demographic modeling efforts (Center for Whale Research 2020). We fit separate smooth terms to male and female EPRs from whales aged 0-60 (Figure 1). We used the raw residuals (observed EPR minus mean EPR estimated by the spline fit) as the basis for defining body condition classes. Ages of a few mature Southern Resident killer whale females that were reproductive when monitoring began in the 1970s are not known precisely, so we calculated residuals for those whales by subtracting observed EPRs from the mean EPR of whales age $60+$. We aggregated the residuals of all EPR measurements from all pods across all years and split that distribution into five equal quantiles, representing the age- and sexnormalized body condition classes to be used in the multi-state model, with body condition class $1(\mathrm{BC} 1)$ being the lowest $20 \%$ quantile and BC 5 being the highest $20 \%$ quantile. Finally, we created a matrix of individuals' body condition classes by year, including unsampled years 20092012 and 2014. In unsampled years, and in years where a whale was not photographed despite survey effort, individual condition was logged as 'NA'. Known deaths from the annual census (Center for Whale Research 2020) were also included in the matrix to facilitate estimation of both age/sex- and body condition-specific mortality probabilities. Because photogrammetry data were collected in September of each year, we considered deaths that occurred between October and the following September to belong to the following survey year. For example, if a whale was measured in September 2016, and died in November 2016, we logged that death in the following time step of the condition matrix, 2017, to allow the model to account for the transition from the condition measured in September 2016 to death. Two known anthropogenic-related deaths
(whales J34 and L95) were not included in the model, and the condition matrix for those whales was left as unknown ('NA') after their last measurements, to prevent them from influencing mortality probabilities for their respective body condition classes prior to death.

## Statistical model

We developed a Bayesian multi-state modeling framework to evaluate changes in body condition between years and the probability of mortality of different condition classes, after accounting for differences in mortality by age and sex. All modeling was performed in JAGS via R (Plummer 2003) and built upon previous multi-state modeling approaches (Kery and Schaub 2012). The model estimated annual transition probabilities between body condition classes, as well as transitions from each body condition class to death, which are the condition-specific mortality probabilities. An increase of one condition class (e.g. BC 1 to BC 2 ; BC 3 to BC 4 ) was considered 'Growth' (G). Increases of two or more condition classes were considered multiple single Growth steps and their probabilities were therefore exponentiated (e.g. BC 1 to $\mathrm{BC} 3=\mathrm{G}^{2}$; BC 1 to $\operatorname{BC} 4=G^{3}$ ). Remaining in the same condition class in two sequential years was considered 'Stable' (S). A decrease of one condition class was considered 'Decline' (D) and decreases of two of more condition classes were exponentiated as with Growth transitions. The advantages of using power functions for the G and D elements are that the number of parameters is reduced relative to an unconstrained matrix, and transitioning across multiple steps is constrained to be less likely than transitioning a single step. In order to make population-level inferences from individual changes in condition, all animals transitioning in the same direction and magnitude contributed to the same transition probabilities, regardless of their starting condition class:

|  | $B C 1$ | $B C 2$ | $B C 3$ | $B C 4$ | $B C 5$ | Dead |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $B C 1$ | $S_{t}$ | $G_{t}$ | $G_{t}^{2}$ | $G_{t}^{3}$ | $G_{t}^{4}$ | $M_{1_{i, t}}$ |
| $B C 2$ | $D_{t}$ | $S_{t}$ | $G_{t}$ | $G_{t}^{2}$ | $G_{t}^{3}$ | $M_{2_{i, t}}$ |
| $B C 3$ | $D_{t}^{2}$ | $D_{t}$ | $S_{t}$ | $G_{t}$ | $G_{t}^{2}$ | $M_{3_{i, t}}$ |
| $B C 4$ | $D_{t}^{3}$ | $D_{t}^{2}$ | $D_{t}$ | $S_{t}$ | $G_{t}$ | $M_{4_{i, t}}$ |
| $B C 5$ | $D_{t}^{4}$ | $D_{t}^{3}$ | $D_{t}^{2}$ | $D_{t}$ | $S_{t}$ | $M_{5_{i, t}}$ |
| Dead | 0 | 0 | 0 | 0 | 0 | 1 |

where rows are the condition class in year $t-1$, columns are the condition class in year $t$, and the matrix is populated by transition probabilities for year $t$. To make the sum of each row equal to 1 , we normalized each row by dividing each element by its row sum (e.g. Cobb \& Chen 2003; Liu et al. 2008). Mortality probabilities $M$ were dependent on an individual whale's age, sex, and body condition. As a result, differences in mortality probability based on age, sex, and body condition slightly affected transition probabilities during row normalization. This can be interpreted as making transition probabilities between condition classes conditional upon a whale surviving.

Mortality probability was estimated in two steps: first based on the age and sex of a whale and then based on the condition class of that whale. We assigned an age class to each whale at each time step in the model, following previous classifications used for SRKW demographic modeling (Ward et al. 2013). Both males and females age 0-2 were defined as calves, and 2-10 as juveniles. Females age 10-44 were defined as young females and 44+ as old females. Males age 10-22 were defined as young males and $22+$ as old males (Figure 1). The baseline mortality probability for whales in each age class was defined as:

$$
M_{\text {Base }_{a}} \sim N\left[\operatorname{logit}\left(\widehat{M}_{\text {Base }}\right), \sigma\right]
$$

$$
\widehat{M}_{\text {Base }} \sim U[0,1]
$$

where $M_{\text {Base }}$ is the baseline mortality probability for a whale in age class $a$ (of the 6 age / sex classes defined above), which is normally distributed around the overall mean mortality probability, $\widehat{M}_{\text {Base }}$, with variance $\sigma$ in logit space. We then added a random effect of body condition such that the mortality probability of a whale at a given time step was calculated as:

$$
\begin{gathered}
M_{i, t}=\text { inv. } \operatorname{logit}\left(M_{\text {Base }_{i, t}}+M_{b c_{i, t}}\right) \\
M_{b c} \sim N[0, \sigma]
\end{gathered}
$$

where $M$ is the mortality probability (in proportional space) for whale $i$ at time $t, M_{\text {Base }}$ is the age-specific baseline mortality probability (in logit space) for whale $i$ given its age and sex class at time $t$, and $M_{b c}$ is the condition-specific effect (in logit space) on baseline mortality for whale $i$ given its body condition class $b c$ at time $t . M_{b c}$ for body condition class $b c(1-5)$ is normally distributed around zero with variance $\sigma$ in logit space. After applying the random effect of body condition to the whale's baseline mortality probability, that sum is converted to proportional space using the inverse logit transformation.

To incorporate salmon abundance covariates into the model we used a cumulative logit transformation to allow covariates to have independent relationships to Growth and Decline transition probabilities while remaining bounded by $[0,1]$ in proportional space. For Growth and Decline transitions we used the following equation:

$$
\text { Transition }_{c, t}=e^{\text {intercept }_{c}+\text { slope }_{c} * \text { covariate }_{t}+\varepsilon_{c, t}}
$$

Where Transition is the uncorrected transition probability in cumulative logit space of transition type $c$ (i.e. G or D) at time $t$, intercept and slope are the linear relationship terms for each transition type $c$, covariate is the salmon index at time $t$, and $\varepsilon$ is the residual error around the linear fit for transition type $c$ at time $t$, with

$$
\varepsilon_{c, t} \sim N[0, \sigma]
$$

where the $\varepsilon$ terms for each transition type $c$ are normally distributed around zero with variance $\sigma$. In the cumulative logit transformation, one parameter must be fixed at 1 for identifiability, which we applied to the probability of Stable condition (S):

$$
\text { Transition }_{S, t}=1
$$

The uncorrected transition probabilities are then transformed to proportional space so that they are bounded by $[0,1]$ :

$$
\text { Prob }_{c, t}=\frac{\text { Transition }_{c, t}}{\sum_{i} \text { Transition }_{t}}
$$

where $\operatorname{Prob}$ is the corrected probability for each transition type $c(\mathrm{G}, \mathrm{D}$, and S$)$ at time $t$.

## Salmon covariates

We evaluated 7 different Chinook salmon abundance indices to identify potential relationships between SRKW body condition and prey availability. We only considered Chinook salmon
given the reported importance of Chinook to SRKW life history and reproductive success (Ward et al. 2009, Ford et al. 2010). We used estimates of Chinook salmon abundance from a model used to manage salmon harvest (Fishery Regulation Assessment Model; FRAM) (Pacific Fishery Management Council 2008). The FRAM model estimates the abundance of multiple west coast salmon populations (or 'stocks') available to fisheries, and its outputs were recently synthesized with Chinook spatio-temporal distribution models to generate indices of Chinook available to killer whales by area, year, and season (Pacific Fishery Management Council 2020).

We used 3 stock-specific and 4 area-specific Chinook indices (Pacific Fishery Management Council 2020). In this framework, estimates of Chinook are generated by season, corresponding to the seasons in the FRAM model (Oct - Apr, May - Jun, Jul - Sep). For all analyses, we used estimated starting abundances on July $1^{\text {st }}$ of each year. SRKW are imaged in September each year, so this summer index of abundance provides the closest match to the true prey availability experienced by whales prior to condition measurements. Furthermore, condition at the time of measurement is unlikely to represent the availability of prey more than a few months prior, as SRKW condition is known to fluctuate seasonally, presumably in response to foraging opportunities (Fearnbach et al. 2018). We focused on 3 of the larger stock-specific indices (Fraser River, Columbia River, and Puget Sound), and included all modeled stock abundances originating from those tributaries (Table S2). The 4 area-specific indices we used were North of Cape Falcon (NOF), Oregon (OR), the Salish Sea (Salish), and Southwest Vancouver Island (SWVI) (Pacific Fishery Management Council 2020). These area-specific indices summed the model estimated abundances of all Chinook salmon from all index stocks that were estimated to be present.

Transition probabilities within the model were related to the salmon index of the year that the whales were transitioning into. For example, the probability of growth (G) from condition class in September 2014 to condition class in September 2015 was linked to estimated Chinook abundance on July $1^{\text {st }}$ of 2015. Given the observed differences in body condition trends between SRKW pods, we ran J, K, and L pods through the model separately, each with the same 7 candidate covariates to identify potential relationships between each pod and various salmon indices. To determine whether there was support for the inclusion of covariates on transition probabilities, we also considered a null model (condition transition probabilities fixed across all years) and a time-only model (condition transition probabilities estimated independently each year with no covariate. Given the relatively small number of deaths that occurred during the study period, and previous studies that have assumed shared mortality probabilities across pods (Ward et al. 2013), we also ran null and time-only models for all pods combined to estimate population-wide mortality probabilities with body condition effects. For each model we ran 3 chains of 100,000 iterations each, with a burn-in of 50,000 iterations and thinning of 50 for a total of 3,000 samples from the posterior distribution. We used non-informative uniform priors for all parameters (Mitchell and Beauchamp 1988), and confirmed model convergence using potential scale reduction factors (Gelman and Rubin 1992) (all parameters PSRF < 1.05) and visual inspection of chain convergence.

## Model Selection

To identify which (if any) Chinook salmon covariates best predicted SRKW body condition transitions, we used a K-fold cross validation approach (Vehtari et al. 2017). There are many
different ways to split training and test data sets for cross validation, depending on the goals of inference. Because our focus is on the temporal aspect, and in developing tools for making short term future predictions of body condition, we treated data from each year iteratively as a 'fold'. For each pod and covariate combination, we ran the multistate condition transition model once with each year of observed condition data held out ( $\mathrm{n}=7$ years), using the remaining years of observed condition data to fit the estimated condition transition probabilities and covariate relationships. We then calculated the expected log pointwise predictive density (ELPD) across all held out years of observed body conditions based on the conditions in the previous year and the model-estimated transition probabilities, following (Vehtari et al. 2017). We performed Kfold Cross Validation for each of the pod and covariate combinations, as well as for each pod with the null and time-only models described above. In addition to the computing the ELPD for each model (models with the highest ELPD receive the highest data support), we calculated the standard error - which is useful in quantifying the uncertainty associated with model selection (Vehtari et al. 2017).

## Results

In the 7 sampled years between 2008 and 2019, a total of 473 measurements of body condition were collected from 99 whales, which were used in our analyses. We recorded a median of 5 years of body condition measurements for each whale (range 1-7). A total of 47 deaths and 33 births were documented in SRKWs between 2008 and 2019, while a total of 29 deaths and 15 births were documented in SRKWs during the same 7 years as the aerial photogrammetry sampling (Center for Whale Research 2020).

In general. K-fold Cross Validation from our Bayesian models suggested that killer whale body condition is better predicted when salmon covariates are included, relative to models without salmon (J and L pods, Table S1). For models with salmon included, the standard errors of the ELPD values exceeded the difference in ELPD values among candidate models, which makes it challenging to confidently select one best-fit model. Consequently, we also report the secondbest fit model for each pod (Figures S1-S3). Due to the complexities of our model and the number of parameters, we present both the raw estimated transition probabilities, as well as aggregated Stable and Growth transition probabilities. This grouping represents a 'Positive' transition group that may be more useful for managers targeted at preventing condition declines and maintaining stable or increasing condition.

Fraser River Chinook was the best predictor of J pod condition transitions (Figure 2, Table S1), although the ELPD values of the Salish Sea area-based Chinook abundance model fit (which includes a large proportion of the Fraser River stock) was almost identical. J Pod had a significant negative relationship between Fraser River Chinook abundance and the probability of declining condition (Decline), with $95.3 \%$ of posterior draws for the slope term in the cumulative logit regression $<0$. There was no clear relationship between Fraser River Chinook abundance and the probability of increasing condition (Growth) ( $38.5 \%$ of posterior draws $>0$ ), and while the probability of Stable condition appears to have a positive relationship with Fraser River Chinook, a slope term for S is not explicitly calculated in the cumulative logit regression. However, as the sum of the probabilities of Growth and Stable condition is equal to 1 minus the probability of Decline, we can infer that there is a positive relationship between Fraser River Chinook and Positive condition transitions (Growth or Stable condition) (Figure 2). When Fraser

River Chinook salmon abundance was above 750,000 fish, J pod whales had a greater than 0.86 median probability of stable or increasing condition. That probability decreased at lower Fraser River Chinook abundance, to a minimum 0.37 median probability of increasing or stable condition when Fraser River Chinook abundance fell to 347,000 fish.

The best fit model for L pod included Chinook Salmon from Puget Sound, and nearly all models with salmon included outperformed the null models (Table S1). There was moderate support for a negative relationship between Puget Sound Chinook abundance and the probability of declining condition, with $88 \%$ of posterior draws for the slope $<0$. Similar to the results for J pod, there was no clear relationship between this index of salmon abundance and the probability of increasing condition ( $56.9 \%$ of posterior draws $>0$ ). Nevertheless, when Puget Sound Chinook abundance was above 399,000 fish during the study period, L pod whales had a 0.82 0.89 median probability of stable or increasing condition. At the second-lowest Puget Sound Chinook abundance during the study period, 235,000 fish in 2015 , L pod whales had a 0.32 median probability of stable or increasing condition. The major deviation from the positive linear relationship between Puget Sound Chinook abundance and condition transitions occurred in 2014, when Puget Sound Chinook was at its lowest point during the study period (208,000 fish), but L pod whales had a 0.60 median probability of stable or increasing condition. Apart from Puget Sound Chinook, all other models for L pod that included salmon covariates (both stockspecific and area-based abundance) produced potentially spurious results, where higher salmon abundance was associated with declining condition (e.g. Figure S3).

Unlike J and L pods, the best-fit model for K pod did not include salmon as a covariate, and transition probabilities were held constant across years. In this null model, the median fixed probability of increasing condition (Growth) was 0.40 ( $95 \%$ highest posterior density intervals [HPDIs]: $0.33-0.47)$. The median probability of Decline was $0.31(0.25-0.37)$, and the median probability of Stable condition was $0.29(0.21-0.38)$. The second best-fit model for $K$ pod included Puget Sound Chinook abundance, however we note that this covariate relationship produced relatively constant condition transitions across years (Figure S2). Nevertheless, there was a significant positive relationship between Puget Sound Chinook abundance and the probability of increasing condition, with $94.93 \%$ of posterior draws for the slope $>0$. There was no clear relationship between Puget Sound Chinook abundance and the probability of declining condition ( $22.6 \%$ of draws $<0$ ), and the probability of stable condition decreased with increasing Chinook abundance (Figure S2). When Puget Sound Chinook abundance was above 399,000 fish, $K$ pod whales had a median $0.43-0.50$ probability of increasing condition. In contrast, when Puget Sound Chinook abundance was at a low of 208,000 , K pod whales had a median 0.14 probability of increasing condition. However, the probability of the management-relevant combined Growth and Stable condition remained relatively constant across the study period (median $0.68-0.78$ probability; Figure S2).

While observations of body condition provided a relatively large sample size for estimating transition probabilities, deaths were relatively uncommon during the 12-year study period. Consequently, we estimated the effects of age, sex and body condition on mortality probabilities by pooling all pods together and running models without covariates (null and time-only). There were 25 total deaths of whales that also had measurements of body condition in at least one year
during the study period ( 12 in J pod, 3 in K pod, and 10 in L pod). 15 of those deaths occurred in the time step immediately following a body condition measurement. With data from all pods combined, the null model had a higher ELPD score than the time only model (Table S1) and was therefore used for estimates of mortality probability. The median expected mortality probabilities for whales in each age/sex and body condition class are reported in Table 2. The expected mortality probability of whales in body condition class 1 was 2-3 times higher than other body condition classes (Figure 3, Table 2). Mortality probability decreased in condition class 2, was lowest in condition classes 3 and 4, and increased slightly in condition class 5 to levels similar to condition class 2. For example, based on the model estimates, a Young Female whale has expected mortality probabilities of: BC1 0.03 (0.009-0.081); BC2 0.014 (0.003-0.043); BC3 0.009 (0.001-0.033); BC4 0.01 (0.001-0.033); BC5 0.017 ( $0.005-0.048)$. Of the whales that died during the study period, condition class 1 whales died soonest after their final condition measurement (mean 169 days), while the time between measurement and estimated death roughly increased with condition class: mean $456,790,572$, and 905 days for classes 2-5, respectively (Figure 4).

## Discussion

The Southern Resident killer whale population offers a unique study opportunity for individualbased body condition monitoring, providing a robust framework that can be extended to other marine and terrestrial populations. Due to the small population size, intensive demographic monitoring, and known fates of virtually every individual, paired with annual photogrammetry measurements of most of the population, we were able to make direct estimates of the relationship between individual salmon stocks and SRKW condition, and relate condition to
survival probability. While small demographic fluctuations limit statistical power for identifying the influence of covariates such as prey abundance, aerial photogrammetry allows for more individuals to be sampled in each year and repeatedly sampled across years, increasing power to evaluate changes in body condition against possible drivers. In this case, we obtained more than ten times as many observations of body condition as observations of births and deaths in the seven years of data collection. While our time series of condition measurements was relatively short, we posit that with continued annual monitoring this method will provide sufficient statistical power for even finer scale investigations of prey availability and population status (e.g. at the individual stock level rather than tributary-level aggregates). Evaluating changes in body condition over time likely provides more insights into drivers of population health than simply comparing single measures of condition (e.g. annual population mean and variance) to potential covariates, given the ability of long-lived animals such as killer whales to live through bottlenecks in resource availability. In addition, there may be inherent differences in baseline condition between individuals, so evaluating individual changes between years rather than raw condition further accounts for individual variability.

Our cross-validation analyses suggest that, in the case of J and L pods, models including salmon covariates better predicted held-out years of body condition data than models without salmon covariates. Given that salmon managers use the FRAM model to generate pre-season estimates of Chinook abundance by stock, the modeling framework we present here could be used to generate predictions of fall SRKW body condition based on those salmon abundance estimates, quantify short-term risks to the population, and identify potential management interventions. Our model results suggest the strongest correlation between killer whale body condition and prey is
between the SRKW J pod and Chinook salmon returning to the Fraser River. The Salish Sea area-based Chinook index was essentially tied for the best-fit J pod model, which is unsurprising considering the Salish Sea index is typically made up of 40-50\% Fraser-origin Chinook. Over the last decade, when Fraser River Chinook abundance was above 750,000 (estimated FRAM Chinook model abundance on July $1^{\text {st }}$ ), J pod whales had a low chance (less than $14 \%$ ) of declining body condition. Such a target could be used in a management setting to define thresholds supporting the stability and recovery of this population segment. For example, management actions focused on habitat restoration that ensures effective anadromous migration and productivity of Fraser River Chinook stocks could lead to gains in the nutritive condition of J pod whales. In the long-term, increasing urbanization of watersheds (Greene and Beechie 2004), increasing abundance of competing predators (Chasco et al. 2017), and climate change (Crozier et al. 2008) all present substantial threats to Fraser River Chinook abundance.

The only positive, ecologically plausible relationship we found for L pod body condition was with the Puget Sound stock-specific abundance index. This is surprising, given that L pod is rarely in Puget Sound in the summer and spends less time in adjacent inland waters during the summer months than J or K pods (Riera et al. 2019), and Puget Sound origin Chinook are generally smaller and less numerically dominant than other stocks (O'Neill et al. 2014, Pacific Fishery Management Council 2020). However, L pod spends more time during the summer months in the western strait of Juan de Fuca than J or K pods (Riera et al. 2019), and may be targeting Puget Sound Chinook as they migrate from their open ocean phase towards spawning tributaries. The somewhat unique oceanic distribution of Puget Sound Chinook along the west coast of Vancouver Island (Weitkamp 2010, Shelton et al. 2019) may provide a reliable prey
base in areas or times when more dominant stocks (Columbia and Fraser rivers) are less abundant. The relationship between L pod body condition transitions and Puget Sound Chinook abundance was weaker than the relationship between J pod and Fraser River Chinook. It is possible that L pod targets Chinook from a variety of stocks as they enter the strait of Juan de Fuca, which could obscure the signal of the Puget Sound Chinook's influence on L pod body condition. However, L pod body condition was negatively correlated to all other stock-specific and area-based indices, including all Chinook salmon present in the Southwest Vancouver Island region, which presumably would be a better representation of Chinook availability at the mouth of the strait of Juan de Fuca. Previous analyses examining the influence of specific Chinook stocks on SRKW demographic rates found a significant relationship between SRKW fecundity and both Puget Sound and Fraser River Chinook abundance (Vélez-Espino et al. 2014), which further indicates the potential importance of these stocks to the SRKW population.

The best-fit model for K pod had fixed body condition transition probabilities across time and included no salmon covariate. K pod may forage on a diverse assemblage of prey that is not easily captured in either stock-specific or area-based indices of Chinook abundance. However, the second best-fit model for K pod included Puget Sound Chinook and suggested a positive relationship between Chinook abundance and the probability of increasing body condition. Additional studies of the fine scale distribution of Puget Sound Chinook along Vancouver Island and the Washington coast, and their representation in the diets of L and K pod whales during summer months could improve our understanding of the importance of this stock to SRKW population health. The major caveat to our findings is that body condition is known to fluctuate over a period of several months (Fearnbach et al. 2019). The three SRKW pods forage on other
salmon stocks in winter and spring months (Hanson et al. 2010), but the September body condition metrics, and therefore the results of our analyses, most likely reflect the effects of the summer foraging period in the Salish Sea.

In addition to demonstrating the link between salmon abundance and body condition of killer whales, our model results show that whales in poor condition are more likely to die. Our estimated baseline mortality rates of whales in different age and sex classes are generally in line with previous findings (Ward et al. 2013), with old males and females experiencing the highest mortality probabilities, and calves experiencing slightly elevated mortality probabilities compared to juveniles and young whales. Our model estimated somewhat higher mortality probabilities for old females, and lower for old males, calves, and juveniles than previous analyses (Ward et al. 2013). These small differences are most likely due to the shorter time series of deaths included in our study (2008-2019 versus 1979-2010) and the exclusion of whales that did not have body condition measurements, although we cannot rule out changes in mortality probability by age and sex class in recent years. Whales in condition class 1 had a mortality probability roughly 2-3 times higher than whales in condition classes 2-5. Interestingly, condition class 5 whales had a slightly elevated mortality probability similar to condition class 2 whales. The two whales that were observed in condition class 5 at the time step immediately prior to death died 317 (L53) and 349 (J14) days after being imaged, and may have experienced a substantial, unrecorded decline in condition during that almost year-long period. Furthermore, while we did account for age and sex effects on mortality probability, there are other factors aside from age, sex, and nutritive condition that may contribute to mortality probabilities, such as the presence or condition of other whales in a matriline (Foster et al. 2012, Nattrass et al. 2019).

The majority of whales that died shortly after being imaged were in condition class 1 (very poor condition), while deaths of higher condition class whales typically occurred longer after their last measurement (Figure 4). This further supports the conclusion that whales in condition class 1 have an elevated mortality probability and suggests that aerial photogrammetry measurements may be able to identify whales most at risk of death in the near future.

Interestingly, changes in condition for animals from J and L pod were best explained by Chinook indices that are negatively correlated with one another (Figure S4), while K pod condition was best explained by constant transition probabilities (or possibly Puget Sound Chinook, similar to L pod). Our findings suggest that the three pods behave very differently in terms of body condition fluctuations, which are likely driven by independent foraging strategies. Recent analyses of SRKW demographic data attempted to relate births and deaths to a wide range of Chinook salmon area-based indices (including several of the area-based indices used in this study), but found no significant relationships (Pacific Fishery Management Council 2020). Our results indicate that it may be advantageous for similar future analyses of demographic fluctuations to consider the three SRKW pods separately. Furthermore, given the differences in important prey indices reported here, it may be more effective for management strategies to treat the population of SRKWs as multiple management units, as the most effective management actions would likely be very different for each pod based on our findings.

In addition to identifying target prey abundance levels to support SRKW recovery, aerial photogrammetry can provide an early warning system that has the potential to serve as the basis for dynamic and adaptive management strategies. In an endangered population that had only 73
remaining individuals as of 2019, demographic casualties such as the death of a reproductive female or a year with no successful births can potentially have catastrophic consequences for population viability. Management actions that respond to these demographic casualties as opposed to preventing them may be insufficient to support population recovery. Our findings show that aerial photogrammetry can be used to identify at-risk individual whales, as well as to collect an overall metric of population health prior to mortality events that could be used to inform management actions. For example, if a large portion of the population is recorded in body condition class 1 during September (e.g. more than $20 \%$ of the population, or some threshold decided upon by managers), then fishery actions could be considered to increase prey availability for SRKW pods over the next year. Some actions that may result in an increase in Fraser Chinook abundances include spatio-temporal closures in areas of high Fraser Chinook encounter rates or mark-selective regulations, as a high proportion of the Fraser stock aggregate is unmarked. However, we note that the predicted fishing mortalities on Chinook are thought to be relatively low compared to the total cohort size (Pacific Fishery Management Council 2020) and that proactive strategies to increase Chinook abundance such as habitat restoration, reducing predator-related mortality, and increased production may provide the greatest benefit to overall Chinook abundance (Greene and Beechie 2004, Crozier et al. 2008, Chasco et al. 2017). These approaches could be implemented at the pod level where, for example, if individuals from K and L pods are in good condition while J pod individuals are in poor condition, management action could be taken to increase Fraser River Chinook availability over the coming year. These assessments of condition could be done in near-real time with a lag of less than 3 months, rapidly informing upcoming management strategies or allowing for interventions at the individual level. In addition to influencing survivorship, body condition is likely also tied to fecundity in killer
whales (Ward et al. 2009). Future work should examine the relationship between reproductive success in the SRKW population and observed body condition, which would allow for a full evaluation of the influence of individual condition on overall population viability and support further modeling and projection efforts to weigh the efficacy of candidate management strategies. In addition, monitoring body condition in other seasons could provide insights into prey populations that may be important to the SRKW population in winter and spring months. As the time series of condition measurements grows it may be possible to evaluate the relationship between SRKW condition and finer scale Chinook stock groupings and potentially other prey species.

It may not be possible to apply the approach used in this study to larger, wide ranging populations of marine mammals where repeated measurements of individuals and samples from a large portion of the population are not feasible. Instead, the average body condition of a random sample of the population may be achievable and, based on our findings, can likely serve as a proxy for short-term, relative population health. In addition, we posit that rapid changes in average body condition within a population can be used as an early-warning indicator of upcoming demographic fluctuations, given our findings that individuals in poor conditions have higher mortality probabilities. The use of body condition as an indicator of population health could be further tested in cetacean populations that have long-term photogrammetry datasets and experience substantial population fluctuations, such as eastern north Pacific gray whales (Perryman and Lynn 2002), validating its use as a preceding signal of demographic impacts and supporting the development of adaptive management strategies.

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JDS: Analysis conceptualization, data analysis, manuscript writing \& editing
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## Data Availability:

Data and code to run multi-state models can be found at: https://github.com/stewart6/SRKWMultiState

## Tables and Figures

Table 1. Number of Southern Resident killer whales measured using aerial photogrammetry in September of each study year, and the percentage of each pod imaged in parentheses.

| Year | J Pod | K Pod | L Pod |
| :---: | :---: | :---: | :---: |
| 2008 | $23(92.0 \%)$ | $18(94.7 \%)$ | $19(46.3 \%)$ |
| 2013 | $25(96.2 \%)$ | $18(94.7 \%)$ | $25(67.6 \%)$ |
| 2015 | $27(100 \%)$ | $19(100 \%)$ | $26(74.3 \%)$ |
| 2016 | $28(96.6 \%)$ | $19(100 \%)$ | $35(100 \%)$ |
| 2017 | $22(91.7 \%)$ | $9(50.0 \%)$ | $30(85.7 \%)$ |
| 2018 | $23(100 \%)$ | $18(100 \%)$ | $29(85.3 \%)$ |
| 2019 | $22(100 \%)$ | $17(100 \%)$ | $21(61.8 \%)$ |

811
812
813

|  |  |  |  |  |  |
| ---: | :--- | :--- | :--- | :--- | :--- |
| Age/Sex Class | BC 1 | BC 2 | BC 3 | BC 4 | BC 5 |
| Calf | 0.04 | 0.02 | 0.01 | 0.01 | 0.02 |
|  | $(0.004-0.177)$ | $(0.001-0.085)$ | $(0.001-0.066)$ | $(0.001-0.069)$ | $(0.002-0.105)$ |
| Juvenile | 0.02 | 0.01 | 0.01 | 0.01 | 0.01 |
|  | $(0.003-0.060)$ | $(0.001-0.030)$ | $(0.000-0.025)$ | $(0.000-0.025)$ | $(0.002-0.037)$ |
| Young Female | 0.03 | 0.01 | 0.01 | 0.01 | 0.02 |
|  | $(0.009-0.081)$ | $(0.003-0.043)$ | $(0.001-0.033)$ | $(0.001-0.033)$ | $(0.005-0.048)$ |
| Old Female | 0.23 | 0.12 | 0.08 | 0.09 | 0.14 |
|  | $(0.069-0.595)$ | $(0.026-0.348)$ | $(0.010-0.261)$ | $(0.011-0.274)$ | $(0.042-0.406)$ |
| Young Male | 0.03 | 0.01 | 0.01 | 0.01 | 0.02 |
|  | $(0.006-0.105)$ | $(0.002-0.052)$ | $(0.001-0.039)$ | $(0.001-0.041)$ | $(0.003-0.062)$ |
| Old Male | 0.16 | 0.08 | 0.05 | 0.06 | 0.09 |
|  | $(0.047-0.432)$ | $(0.018-0.231)$ | $(0.006-0.171)$ | $(0.007-0.173)$ | $(0.026-0.267)$ |

Table 2. Model-estimated mortality probabilities by body condition (BC) and age/sex class for Southern Resident killer whales. Reported values are median estimates with $95 \%$ highest posterior density intervals in parentheses.


Figure 1. Eye patch ratios by age and sex for Southern Resident killer whale individuals from all three pods during the study period. The top panel shows the measured eye patch ratio by age for males (blue) and females (orange). The spline fits for males (blue) and females (orange) were used to define body condition classes based on residuals, while a mean Eye patch ratio was used to calculate residuals for females aged $60+$ that did not have reliable age estimates (see Methods) Vertical dashed lines delineate the age and sex classes used to estimate age- and sex-specific mortality probabilities. The series of images tracks the eye patch ratio (EPR) and body condition class (BC) of adult female J17 from 2015-2018, demonstrating the observed decline in condition preceding her death in summer 2019. The progression of J17's eye patch ratios are highlighted in the top panel in larger, dark orange circles connected by lines. The orange horizontal lines in the far-left image show how the eye patch ratio is calculated (EP bottom divided by EP top), providing a metric of adipose fat behind the cranium as a proxy for nutritive condition.

Figure 2. Body condition transition probabilities for Southern Resident killer whale J (a-d) and L (e-h) pods with best-fit Chinook salmon covariates (Fraser River and Puget Sound, respectively). The best-fit model for K pod did not include a covariate (see Results). Panels show the model-estimated relationships between Chinook salmon abundance and the probability of a Decline in body condition (a,e), and the combined probability of Growth or Stable body condition (b,f). The probability of Growth or Stable condition shown in $b \& f$ is the sum of the posterior distributions for the probability of Growth ( $\mathrm{c}, \mathrm{g}$ ) and the probability of Stable condition (d,h). Put simply, $b=c+d$ and $f=g+h$. Points and vertical bars represent the median estimated transition probability with $95 \%$ Highest Posterior Density Intervals. The light and dark shading represent the $95 \%$ and $50 \%$ HPDIs, respectively, of the model-estimated relationship between salmon covariates and transition probabilities, along with the median estimate of this fit (black line).


Figure 3. Age/sex class- and condition-specific mortality probabilities for Southern Resident killer whales (all pods combined). Calf and Juvenile age classes include both sexes. Violin plots represent the posterior distributions of the effect of age/sex (top) or body condition (bottom) class on mortality probability. Inset boxplots represent the median (black horizontal bar), $50 \%$ HPDI (white box), and $95 \%$ HPDI (vertical black lines). Note that the effects are applied in logit space before transformation to proportional space. See Table 2 for expected mortality probabilities of each age/sex and body condition class combination.

Figure 4. Time between final condition measurement and estimated death for Southern Resident killer whales that died during the 2008-2019 study period. Each density plot represents the estimated number of days between when a whale was last measured and when it died, broken out by the condition class (BC1-5) that whales were last recorded as before death. Points represent the time between final measurement and death for individual whales, color coded by pod and jittered randomly on the $y$ axis.

## Supplementary Information

Table S1. K-fold Cross Validation model selection table. Expected log pointwise predictive density (ELPD) scores with standard errors for all candidate Chinook salmon abundance indices as well as null and time only models for each Southern Resident killer whale pod. Fraser River, Columbia River, and Puget Sound are stock-specific abundance indices, while North of Cape Falcon, Oregon coast, Salish Sea, and Southwest Vancouver Island are area-based Chinook abundance indices. The null model holds transition probabilities constant across years, while the time only model estimates independent annual transition probabilities without the inclusion of a covariate. Null and time only models were also run for all pods combined to estimate a joint mortality probability based on age, sex, and body condition effects. (*) indicate the top two models based on ELPD scores for each pod. Bold values indicate the top model for each pod that is reported in the main text.

| Covariate | J Pod ELPD <br> (SE) | K Pod ELPD <br> (SE) | L Pod ELPD <br> (SE) | All Pods ELPD <br> (SE) |
| :--- | :--- | :--- | :--- | :--- |
| Fraser River | $\mathbf{- 1 8 8 . 9 2}(\mathbf{1 3 . 1 2})^{*}$ | $-106.11(11.01)$ | $-182.7(19.07)$ |  |
| Columbia River | $-190.86(12.82)$ | $-109.77(11.58)$ | $-181.53(19.4)$ |  |
| Puget Sound | $-191.18(12.52)$ | $-103.73(10.39)^{*}$ | $\mathbf{- 1 7 8 . 6 6}(\mathbf{1 8 . 6 1})^{*}$ |  |
| North of Cape Falcon | $-194.47(12.79)$ | $-111.36(11.97)$ | $-179.22(19.16)^{*}$ |  |
| Oregon Coast | $-192.44(12.66)$ | $-108.57(11.32)$ | $-179.57(19.43)$ |  |
| Salish Sea | $-188.94(13.25)^{*}$ | $-107.96(10.95)$ | $-183.78(19.17)$ |  |
| Southwest Vancouver Is. | $-193.32(12.94)$ | $-113.55(12.79)$ | $-181.34(18.96)$ |  |
| Time Only | $-195.89(12.42)$ | $-111.59(12.38)$ | $-182.55(19.09)$ | $-602.55(32.66)$ |
| Null | $-190.42(13.31)$ | $\mathbf{- 1 0 2 . 1 8 ( 1 1 . 3 2 ) *}$ | $-191.97(24.24)$ | $\mathbf{- 5 9 4 . 8 6 ( \mathbf { 3 1 . 7 9 } )}$ |

Table S2. Chinook salmon stock-specific designations. All summer and fall stocks originating within each tributary were aggregated into a single stock-specific abundance index. Each stock is associated with a FRAM Stock Number and Stock Name.

| Present Study Stock Assignment | FRAM Stock Number | Stock Name |
| :---: | :---: | :---: |
| Columbia River | 37 38 39 40 41 42 43 44 45 46 47 48 53 54 67 | UnMarked CR Oregon Hatchery Tule Marked CR Oregon Hatchery Tule UnMarked CR Washington Hatchery Tule Marked CR Washington Hatchery Tule UnMarked Lower Columbia River Wild Marked Lower Columbia River Wild UnMarked CR Bonneville Pool Hatchery Marked CR Bonneville Pool Hatchery UnMarked Columbia R Upriver Summer Marked Columbia R Upriver Summer UnMarked Columbia R Upriver Bright Marked Columbia R Upriver Bright UnMarked Snake River Fall Marked Snake River Fall UnMarked Lower Columbia Naturals |
| Fraser River | $\begin{aligned} & 59 \\ & 60 \\ & 61 \\ & 62 \end{aligned}$ | UnMarked Fraser River Late Marked Fraser River Late UnMarked Fraser River Early Marked Fraser River Early |
| Puget Sou | $\begin{gathered} 1 \\ 2 \\ 7 \\ 8 \\ 9 \\ 13 \\ 14 \\ 15 \\ 16 \\ 17 \\ 18 \\ 19 \\ 20 \\ 21 \\ 22 \\ 23 \\ 24 \\ 25 \\ 26 \\ 27 \\ 28 \end{gathered}$ | UnMarked Nooksack/Samish Fall Marked Nooksack/Samish Fall UnMarked Skagit Summer/Fall Fing Marked Skagit Summer/Fall Fing UnMarked Skagit Summer/Fall Year UnMarked Snohomish Fall Fing Marked Snohomish Fall Fing UnMarked Snohomish Fall Year Marked Snohomish Fall Year UnMarked Stillaguamish Fall Fing Marked Stillaguamish Fall Fing UnMarked Tulalip Fall Fing Marked Tulalip Fall Fing UnMarked Mid PS Fall Fing Marked Mid PS Fall Fing UnMarked UW Accelerated Marked UW Accelerated UnMarked South Puget Sound Fall Fing Marked South Puget Sound Fall Fing UnMarked South Puget Sound Fall Year Marked South Puget Sound Fall Year |

Figure S1. Covariate relationships for Southern Resident killer whale J Pod \& Salish Sea Chinook salmon (second best-fit model): Decline (D), Growth / Stable (G/S), Growth (G), Stable (S). Note that the probability of Growth or Stable condition in the top right panel is the sum of the posterior distributions of the probabilities of Growth (bottom left) and Stable condition (bottom right). Put simply, $P(G S)=P(G)+P(S)$. Points and vertical bars represent the median estimated transition probability with $95 \%$ Highest Posterior Density Intervals, and the light and dark shading represent the $95 \%$ and $50 \%$ HPDI, respectively, of the model-estimated relationship between the Salish Sea Chinook abundance and transition probabilities, along with the median estimate of this fit (black line).

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Figure S2. Covariate relationships for Southern Resident killer whale K Pod \& Puget Sound Chinook salmon (second best-fit model): Decline (D), Growth / Stable (G/S), Growth (G), Stable (S). Note that the probability of Growth or Stable condition in the top right panel is the sum of the posterior distributions of the probabilities of Growth (bottom left) and Stable condition (bottom right). Put simply, $\mathrm{P}(\mathrm{GS})=\mathrm{P}(\mathrm{G})+\mathrm{P}(\mathrm{S})$. Points and vertical bars represent the median estimated transition probability with $95 \%$ Highest Posterior Density Intervals, and the light and dark shading represent the $95 \%$ and $50 \%$ HPDI, respectively, of the model-estimated relationship between the Puget Sound Chinook abundance and transition probabilities, along with the median estimate of this fit (black line).

Figure S3. Covariate relationships for Southern Resident killer whale K Pod \& North of Cape Falcon (NOF) Chinook salmon (second best-fit model): Decline (D), Growth / Stable (G/S), Growth (G), Stable (S). Note that the probability of Growth or Stable condition in the top right panel is the sum of the posterior distributions of the probabilities of Growth (bottom left) and Stable condition (bottom right). Put simply, $\mathrm{P}(\mathrm{GS})=\mathrm{P}(\mathrm{G})+\mathrm{P}(\mathrm{S})$. Points and vertical bars represent the median estimated transition probability with $95 \%$ Highest Posterior Density Intervals, and the light and dark shading represent the $95 \%$ and $50 \%$ HPDI, respectively, of the model-estimated relationship between the NOF area-based Chinook abundance and transition probabilities, along with the median estimate of this fit (black line).


Figure S4. Chinook salmon abundances used as candidate covariates in the Southern Resident killer whale body condition transition models. The plotted abundance indices were generated by dividing the annual abundance for each stock by the mean abundance of that stock for years 2009-2019 in order to plot the salmon data on a common scale. The Columbia River, Fraser River, and Puget Sound are stock-specific abundance indices, while North of Cape Falcon (NOF), Oregon coast (OR), Salish Sea, and Southwest Vancouver Island (SWVI) are area-based Chinook abundance indices, representing total abundance of Chinook salmon from any stock within a specific region. See Methods for more details.

