

Shifts in Southern Resident Killer Whale Phenology in the Salish Sea

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A.K. Ettinger, C. Harvey, J. Samhouri, B. Hanson, C. Emmons, J. Olson, E. Ward

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Introduction

Phenology, or the timing of biological activities such as migration, growth, and reproduction, can have dramatic implications for fitness (Lane et al., 2012; Chuine, 2010). Consumer phenology that is out of step with its resource phenology can cause increased mortality (?) or reduced reproductive success (Post and Forchhammer, 2007). The critical nature of these “matches” or “mismatches” was originally described for fish and zooplankton (Hjort, 1914; Cushing, 1974, 1975), and has received renewed scientific interest as phenological shifts have been increasingly observed in conjunction with recent climate change (Durant et al., 2007).

Despite its importance, phenology of many organisms, even those of conservation concern, remains poorly understood and is rarely quantified, especially for marine organisms. A recent meta-analysis found that shifts in marine phenology are at least as dramatic as those observed in terrestrial systems (e.g. days per decade) (Poloczanska et al., 2013). The abundance of critical resources is more often a focus of natural resource management, yet the timing of resource peaks can be at least as important to consumers (Hipfner, 2008).

Southern resident killer whales (SRKWs, *Orcinus orca*) are a federally endangered population that spends time in the inland waters of Washington State, USA, and British Columbia, Canada. They have received widespread scientific and public attention in recent years as their numbers have declined (e.g., Seattle Times articles, Lusseau et al., 2009; Larson et al., 2018; Olson et al., 2018). Insufficient prey availability is believed to be one of the primary threats to this population, along with vessel traffic and pollutants (Krahn et al., 2007; Lusseau et al., 2009; Hanson et al., 2010). SRKWs differ from many orca whales in that their primary prey are salmon (*Oncorhynchus* species), especially Chinook salmon (*Oncorhynchus tshawytscha* Hanson et al., 2010). SRKWs use inland waters to hunt for their prey when they are aggregated and locally highly abundant. Salmon have a distinct seasonality to their migration patterns, and SRKWs also vary seasonally in their use of inland waters: they travel between summer and winter core areas that can be separated by thousands of kilometers (??).

In recent decades, the abundance and phenology of the favored prey of SRKWs, salmon, has shifted in the western United States (Weinheimer et al., 2017; Reed et al., 2011; Ford et al., 2006; Satterthwaite et al., 2014)(add Nelson for chinook hatchery release timing), though patterns vary by species and location. We would therefore expect SRKW phenology to have shifted during this time, if prey is a primary driver of their activity in inland waters. If SRKW phenology has not shifted at a rate consistent with phenological shifts in

their prey, this mismatch could exacerbate the low prey availability they experience.

Here, we seek to quantify seasonal variation in SRKW activity and the extent to which these seasonal patterns have shifted over the past four decades. Specifically, we ask:

1. Has the timing of SRKW activity (phenology) shifted in the Salish Sea?
2. If there have been phenological shifts in SRKW activity, do these shifts coincide with shifts in phenology of their prey, salmon (*Oncorhynchus* species)?

Methods

Focal species description

: Southern resident killer whales are a population of killer whales that inhabit coastal waters from central California to northern British Columbia. During the summer months they are often seen in inland waters of Washington and southern British Columbia (Fig. 1). Southern residents are considered distinct from another population of fish-eating killer whales, known as the northern resident killer whales (NRKWs), whose distribution is further north, and from co-occurring ‘transient’ killer whales, which feed primarily on marine mammals (Bigg 1982). Southern resident killer whales have declined dramatically since the 1970s, and are now listed as endangered under the Canadian Species at Risk Act (SARA) and the US Endangered Species Act (ESA). Threats to this population include small population size, chemical contamination, disturbance from boat traffic, and insufficient prey availability (Holt et al. 2009, Lusseau et al. 2009, Noren et al. 2009, Williams et al. 2009, Ward et al. 2009, Ford et al. 2009). The SRKW population is composed of three subgroups, or pods, identified as J, K, and L, which are matrilineally related, cohesive and stable social groups. Individuals rarely disperse from their natal pods (Bigg et al. 1990).

Data

Southern resident killer whales: To quantify SRKW seasonal phenology over time, we used the OrcaMaster Database for Whale Sighting Data (Whale Museum), comprised of data from five main sources, including public sightings networks (e.g., OrcaNetwork), commercial whale watch data, and scientific surveys (e.g., SPOT data from satellite tracking units) (Olson et al., 2018). We used data from 1978-2017, because prior to this time there was no dedicated effort to track SRKW presence in the region (Olson et al., 2018). We used these sighting data to quantify detection of SRKWs in the two core areas: the Central Salish Sea, used primarily by SRKWs from May through September, and Puget Sound proper, visited by SRKWs most commonly from September through January (Olson et al., 2018). We used these seasonal definitions because they are most aligned with mean SRKW seasonal activity patterns over time (Fig 1). We also quantified number of whale days (i.e. days on which whales were observed) within a season and year for each region.

Salmon: To quantify potential shifts in SRKW prey phenology over time, we used two datasets. We used adult salmon return (‘escapement’) data for coho, chum, and chinook salmon in Washington state (<https://wdfw.wa.gov/fishing/management/hatcheries/escapement>). Daily or weekly WDFW data are available for 67 streams going back to 1997 and include wild and hatchery counts. We selected sites located close to Puget Sound or the central Salish Sea (i.e., within XX km) with the greatest available data (i.e., long time series with frequent monitoring), and with relatively large run sizes (range of average counts from trap estimates = 1,400-30,000 for chum, 621 - 11,500 for coho, and 550-13,350 for chinook.) We stress that the particular runs we chose may not be widely represented in SRKW diet, but they represent the best available data for salmon phenology in Washington state of which we are aware.

We also used data from the Albion Chinook and Chum test fisheries, located on the lower Fraser River at Albion, British Columbia, Canada (<https://www.pac.dfo-mpo.gc.ca/fm-gp/fraser/docs/commercial/albionchinook-quinnat-eng.html>), 80-90% of the chinook salmon consumed by SRKWs appear to be from the Fraser River (Hanson et al., 2010).

Analysis

Southern resident killer whales:

To identify trends over time in phenology for SRKWs in the Central Salish Sea and in Puget Sound proper, we summarized first-, last-, and mean- observation dates from 1978 through 2017 in each region.

We quantify pod-specific phenology for J, K, and L pods in the north versus south regions using occupancy models. Occupancy models can estimate jointly species presence and detection probability (p , the probability of detecting at least one individual present at a site) by distinguishing true presence or absence, z (a latent, unobservable state), from observed presence. Occupancy models are composed of a state submodel, which is the model for the ecological process of true presence or absence, and an observation submodel, which links the observations (i.e., whether or not whales were seen) to the state model.

We fit a hierarchical model in which occupancy probability (ψ) was a function of day of year (i.e., we did not fit a dynamic model, but a multi-year model, Royle and Kery 2007), with year and marine area as levels. Occupancy probability was modeled as a semi-parametric, smooth function of day of year ('*day*') using flexible thin-plate spline regression modelling (Strebel et al., 2014). We assumed z , to be a Bernoulli random variable for which 0 signifies absence and 1 is presence. We modeled detection probability (p) as a year- ('*yr*') and marine area- ('*area*') specific probability between 0 and 1. Thus, our occupancy model can be described by the following equations:

Observation model

$$y_{area, yr, day} \sim \text{Binomial}(T_{yr, day, area}, z_{yr, day} * p_{area, yr}) \quad (1)$$

State model

$$z_{yr, day} \sim \text{Bernoulli}(\Psi_{yr, day}) \quad (2)$$

Occupancy models were fit in JAGS, through R2jags (Su and Yajima, 2015) in R, version 3.5.1 (R Core Team, 2018). We fit separate occupancy models within each region (and season, since seasonal use varies by region) for each pod, and estimated annual arrival, departure, and peak occupancy dates with each model. We defined arrival date as the earliest DOY within the season when occupancy probability exceeded 0.5; departure date was the latest DOY within the season when detection probability exceeded 0.5. (Using a threshold probability lower than 0.5 did not qualitatively alter observed trends, Figure SX.)

Add analysis of Lime Kiln observations, a subset of data for which effort has not changed so dramatically: .
Salmon:

We used hierarchical linear models to identify trends over time in first, median, peak, and last dates of salmon adult migration timing.

Results

We found that SRKW phenology has shifted over the past four decades, though not necessarily in a linear fashion. Across the full time span, first-detection dates have gotten earlier by XX days per decade in Puget Sound and have not shifted in the Central Salish Sea (Fig. 2). Last-detection dates have gotten later by XX days in Puget Sound and by XX days per decade in the Upper Salish Sea (Fig. 2). Add trends in whale days.

We found that salmon phenology has shifted as well, though the patterns differ across species and regions. In the central Salish Sea, the return timing of wild chinook in the Fraser River has delayed by 8.0 days per decade (75 percent credible intervals: 5-11 days per decade) for first- observations dates from 1980-2018. Delays in peak return and median return dates are stronger (11.8 and 12.7 days per decade, respectively). Hatchery salmon also showed delays in first and median returns in the central Salish Sea(e.g., chum salmon).

In Puget Sound proper where data were available across more streams and the preferred prey of SRKWs are less known, the most common trend for wild and hatchery salmon was a shift toward earlier returns.

Discussion

The timing of SRKW activity has shifted. Across the full time-series SRKWs, especially J- and L-pods, are arriving earlier in Puget Sound and in the central Salish Sea. SRKWs are spending less time in recent years in the upper Salish Sea. Though the trend across the full time series is earlier first-detection and later last-detection dates, in the last 5-10 years, first-detection dates have gotten later in the upper Salish Sea region.

The timing of adult salmon returns has also shifted. Populations in the central Salish Sea are arriving later, whereas many populations in Puget Sound proper, especially hatchery-origin fish, are arriving earlier.

The timing of SRKW activity in central Salish Sea and in Puget Sound proper appears to be shifting in a manner that differs from shifts in salmon timing. This difference may lead to a mismatch between predator and prey that causes additional stress on SRKW populations, since the timing of resource availability can be as important as the amount of the resource (Brianna's work, Hipfner, 2008)

Observer effort has shifted over time. Its great that so many people are outside looking for whales! Recommend collecting absence data too. This would allow for more robust analyses of whale distributions. Challenge is increased time/money required for database maintenance with this extra data.

Conclusion

Needs/Questions

1. Intro: make a clearer case of the urgency faced by the SRKW pop and therefore the importance of this work
2. What other figures would be helpful?

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Figures

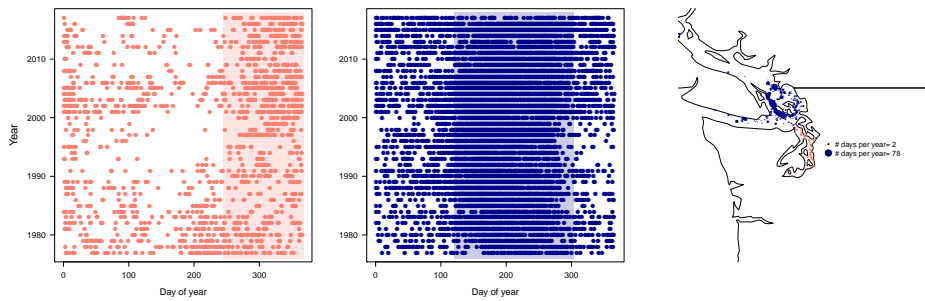


Figure 1: Southern resident killer whale activity in the Upper Salish Sea and Puget Sound varies by season.

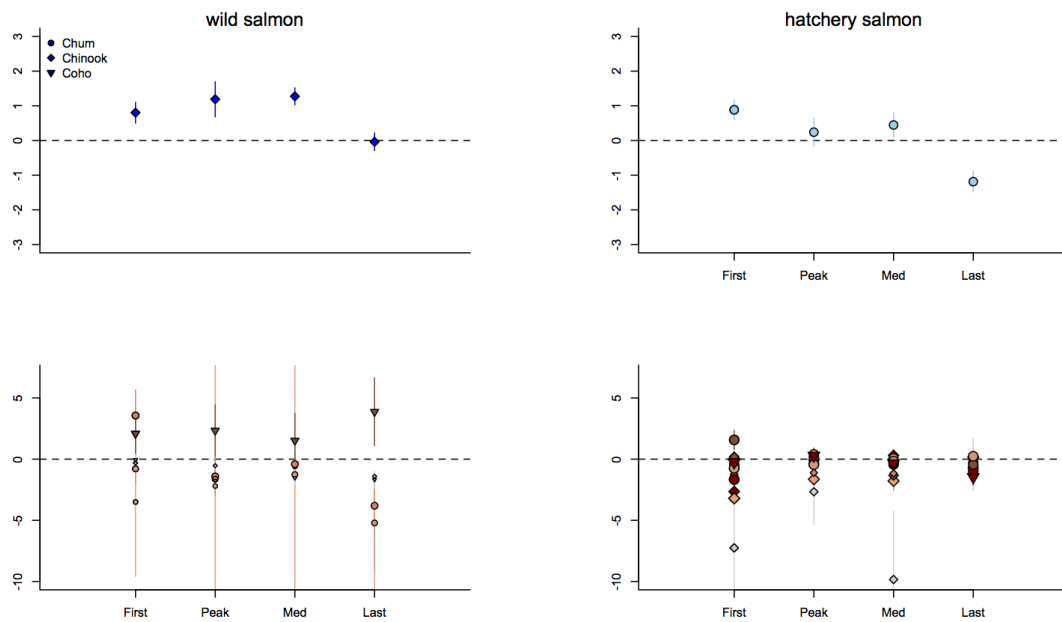


Figure 2: Trends in first-, peak-, and last- observation dates for SRKWs and their prey.