

Shifts in Southern Resident Killer Whale Phenology in the Salish Sea

September 17, 2019

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

Target journal(s): Global change biology, Journal of Applied Ecology

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., -4.4 ± 0.7 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 (Balcomb III and Bigg, 1986; KRAHN et al., 2005).

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 water's of Washington and southern British Columbia (Fig. 2). 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 2). 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 the number of whale days (days on which whales were observed), as well as first-, last-, and mean- observation dates from 1978 through 2017 in each region.

We quantified pod-specific phenology for J, K, and L pods in the Central Salish Sea versus Puget Sound Proper 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 with 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 extracted estimates of 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.)

With increasing public awareness of the plight of SRKWs and with the rise of social media, there has been a dramatic increase in reported sightings of SRKWs since 1978 (Olson et al., 2018). As a presence-only database, trends in the OrcaMaster dataset should be interpreted with care, since they could be due to shifts in effort as well as (or instead of) trends in SRKW activity. For this reason, we report all trends across two different durations: the full dataset (from 1978-2017) and recent years (2002-2017). We use 2002 as a cut-off, to avoid the included a sharp increase in sightings that occurred in 2001, likely influenced by the onset of internet-based sightings platforms that began that year (Olson et al., 2018). Further, because the above occupancy models cannot fully statistically account for changes in effort over time, due to the presence-only nature of the data, we compared phenology estimates from the occupancy models to phenology observed at Lime Kiln state park from 1990 to 2017. This dataset represents a subset of the OrcaMaster database that was collected with consistent observer effort from May through September (Olson et al., 2018).

Quantifying effects of changes in effort: (could move this to supp?)

To better understand how increased effort across the timeseries (i.e., increased numbers of sightings over time) may affect estimates of trends in phenology, we simulated data sets of whale presence during two seasons equivalent to those in our data set (summer, which was 1 May through 31 Sept, or 153 days, and fall, which was 1 October through 1 Feb, or 123 days). We used whale presence probabilities of 0.85 for the Central Salish Sea and 0.6 for Puget Sound (the means in our data set for each region) and kept it constant over 40 simulated years. We then created an observation data set, in which effort (the number of observations), varied. During the low effort time period (years 1-20), the number of observations had a mean of 15 per year for Puget Sound and 104 per year in the Central Salish Sea (matching the means for these regions from 1978-1997 in the OrcaMaster database). During the high effort time period (years 21-40 in our simulated data set), the number of annual observations had a mean of 39 for Puget Sound and 133 for the Central Salish Sea (matching those in the OrcaMaster database from 1998-2017). We then calculated first- and last-observations dates for each simulated year. We ran these simulation 100 times and calculated the difference between the low effort and high effort time periods. We compared these to the mean differences first- and last-observation dates across time periods in the OrcaMaster database, for each region, to understand whether observed changes may be due to changes in effort over time, rather than changes in orca activity. Salmon:

We used hierarchical linear models to identify trends over time in first, median, peak, and last dates of salmon adult migration timing in Puget Sound proper. We treated distinct rivers and species, as well as hatchery versus wild types of the same species, as separate groups in our model. Our model allowed for different trends (slopes) across these separate troupes, estimating both species-level responses (generally yielding more accurate estimates for well-represented groups), and the distribution from which they are drawn, yielding an estimate of the overall response across groups.

Results

We found that SRKW phenology has shifted. Since 2000*, estimated peak occurrence probability in the Central Salish Sea has gotten later for all three pods, at rates ranging from 0.88 to 2.71 days per year (Fig. 2). Trends across the full dataset (1978-2016) were also toward later peak occurrence probability, though they were less dramatic (Fig. 3) and the dramatic increase in effort has likely affected some of these trends (see Supplemental Materials for details). In Puget Sound proper, there has not been a consistent linear trend in peak occurrence since 2000 for any pod (i.e., credible intervals around the slopes encompass 0). The trends across the full time dataset has been toward later peak occurrence for all three pods (Fig. 2). *change to 2002 (as justified in the methods) and get new estimates

Coincident with these phenological trends, the number of whale days has also changed across the time-series (Fig. 3). Across the full dataset, the number of whale days has increased in both regions (and for all pods). At least some of these increasing trends are due to increased effort (see Supplemental Materials). Since 2002, the number of whale days has decreased in the Central Salish Sea, across all pods.

We found that salmon phenology has shifted as well, though the patterns differ across regions (Fig. 4). In the central Salish Sea, the return timing of chinook in the Fraser River has delayed by 0.80 per year (80% credible intervals: 0.5-1.1 days per year) for first-observations dates from 1980-2018 (Fig 4A). Delays in peak return and median return dates are stronger (1.2 and 1.3 days per decade, respectively). In Puget Sound proper, where data were available across more streams and the preferred prey of SRKWs are more poorly understood, we observed a shift toward earlier returns (Fig. 4B).

Discussion

The timing of SRKW activity has shifted, and there are many possible reasons for their shifting phenology. Changes in phenology widely reported and often attributed to climate change (Climate change? Rates observed here are more dramatic than many shifts attributed to cc). Impossible to definitely identify drivers of these shifts.

It is possible that phenological shifts found in SRKWs can be attributed to changes in their prey. Consistent with this...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.

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.

social reasons for shifts

Conclusion

Questions

1. Currently I report trends for both recent years (since 2002) and the full time series (1978-present). Would it be better to only report on recent years? (Justified using the rationale already described in the methods- internet based reports.)
2. Fig. 2: Do you prefer the data version (with whale days) or the modeled version (with probability of occurrence, Fig. 2Alt)? If Fig. 2Alt, which timespans to include (2008-2017 vs 1998-2007 OR 2008-2017 vs 1978-2007)?
3. Fig. 3: Add linear trend to time series of peak occurrence day of year or no?
4. Fig. 4: salmon: Do we want to show the coefficients from linear models (as shown) or curves of CPUE (similar to figure 2) or something else?
5. Fig. 5: Lime Kiln vs broader Central Salish Sea phenological patterns, as related to chinook in the Fraser River. Other ideas for how to handle this?
6. Color scheme- do you like the color scheme currently (blue vs pink) or would other colors be prettier or more intuitive or better for some other reason?
7. Include simulation methods and results only in supplement?
8. What else should we include in the supplement (see below for a start)?
9. Full year models or seasonal models?

To Do

1. Write Discussion (for 9/24/2019)
2. Supplemental Materials:

- (a) Time series of peak prob. occurrence for K and L pods
- (b) Time series for first- and last- dates when occurrence probability is greater than 0.5 for J,K,L pods
- (c) Expected phenological change due to change in effort alone (simulations)- do this for the recent time span as well?

References

- Balcomb III, K., and M. Bigg. 1986. Population biology of the three resident killer whale pods in puget sound and off southern vancouver island. Behavioral biology of killer whales. Alan R. Liss, New York, New York pages 85–95.
- Chaine, I. 2010. Why does phenology drive species distribution? Philosophical Transactions of the Royal Society B: Biological Sciences 365:3149–3160.
- Cushing, D. 1974. The natural regulation of fish populations. Sea fisheries research .
- Cushing, D. H. 1975. Marine ecology and fisheries. CUP Archive.
- Durant, J. M., D. Hjermann, G. Ottersen, and N. C. Stenseth. 2007. Climate and the match or mismatch between predator requirements and resource availability. Climate research 33:271–283.
- Ford, M. J., H. Fuss, B. Boelts, E. LaHood, J. Hard, and J. Miller. 2006. Changes in run timing and natural smolt production in a naturally spawning coho salmon (*Oncorhynchus kisutch*) population after 60 years of intensive hatchery supplementation. Canadian Journal of Fisheries and Aquatic Sciences 63:2343–2355.
- Hanson, M. B., R. W. Baird, J. K. Ford, J. Hempelmann-Halos, D. M. Van Doornik, J. R. Candy, C. K. Emmons, G. S. Schorr, B. Gisborne, K. L. Ayres, et al. 2010. Species and stock identification of prey consumed by endangered southern resident killer whales in their summer range. Endangered Species Research 11:69–82.
- Hipfner, J. M. 2008. Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. Marine Ecology Progress Series 368:295–304.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern europe viewed in the light of biological research. ICES.
- Krahn, M. M., M. B. Hanson, R. W. Baird, R. H. Boyer, D. G. Burrows, C. K. Emmons, J. K. Ford, L. L. Jones, D. P. Noren, P. S. Ross, et al. 2007. Persistent organic pollutants and stable isotopes in biopsy samples (2004/2006) from southern resident killer whales. Marine pollution bulletin 54:1903–1911.
- KRAHN, M. M., D. P. HERMAN, D. G. BURROWS, P. R. WADE, J. W. DURBAN, M. E. DAHLHEIM, R. G. LEDUC, L. BARRETT-LENNARD, and C. O. MATKIN. 2005. Use of chemical profiles in assessing the feeding ecology of eastern north pacific killer whales. Paper presented by Margaret Krahn to the International Whaling Scientific Committee .
- Lane, J. E., L. E. Kruuk, A. Charmantier, J. O. Murie, and F. S. Dobson. 2012. Delayed phenology and reduced fitness associated with climate change in a wild hibernator. Nature 489:554.
- Larson, S., J. Olsen, and R. Osborne. 2018. Sightings of southern resident killer whales in the salish sea 1976-2014 .
- Lusseau, D., D. E. Bain, R. Williams, and J. C. Smith. 2009. Vessel traffic disrupts the foraging behavior of southern resident killer whales *Orcinus orca*. Endangered Species Research 6:211–221.

- Olson, J. K., J. Wood, R. W. Osborne, L. Barrett-Lennard, and S. Larson. 2018. Sightings of southern resident killer whales in the salish sea 1976–2014: the importance of a long-term opportunistic dataset. *Endangered Species Research* 37:105–118.
- Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K. Brander, J. F. Bruno, L. B. Buckley, M. T. Burrows, et al. 2013. Global imprint of climate change on marine life. *Nature Climate Change* 3:919.
- Post, E., and M. C. Forchhammer. 2007. Climate change reduces reproductive success of an arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B: Biological Sciences* 363:2367–2373.
- R Core Team. 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Reed, T. E., D. E. Schindler, M. J. Hague, D. A. Patterson, E. Meir, R. S. Waples, and S. G. Hinch. 2011. Time to evolve? Potential evolutionary responses of Fraser River sockeye salmon to climate change and effects on persistence. *PLoS One* 6:e20380.
- Satterthwaite, W. H., S. M. Carlson, S. D. Allen-Moran, S. Vincenzi, S. J. Bograd, and B. K. Wells. 2014. Match-mismatch dynamics and the relationship between ocean-entry timing and relative ocean recoveries of central valley fall run chinook salmon. *Marine Ecology Progress Series* 511:237–248.
- Strebel, N., M. Kéry, M. Schaub, and H. Schmid. 2014. Studying phenology by flexible modelling of seasonal detectability peaks. *Methods in Ecology and Evolution* 5:483–490.
- Su, Y.-S., and M. Yajima. 2015. R2jags: Using R to Run 'JAGS'. R package version 0.5-7.
- Weinheimer, J., J. H. Anderson, M. Downen, M. Zimmerman, and T. Johnson. 2017. Monitoring climate impacts: Survival and migration timing of summer chum salmon in salmon creek, washington. *Transactions of the American Fisheries Society* 146:983–995.

Figures

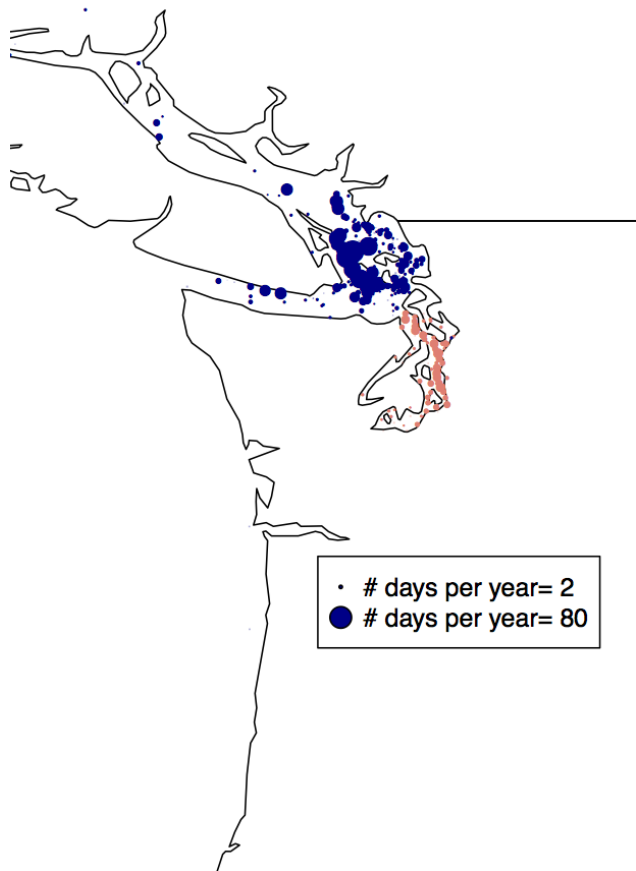


Figure 1: Southern resident killer whale activity varies across two broad regions: the Central Salish Sea and Puget Sound proper.

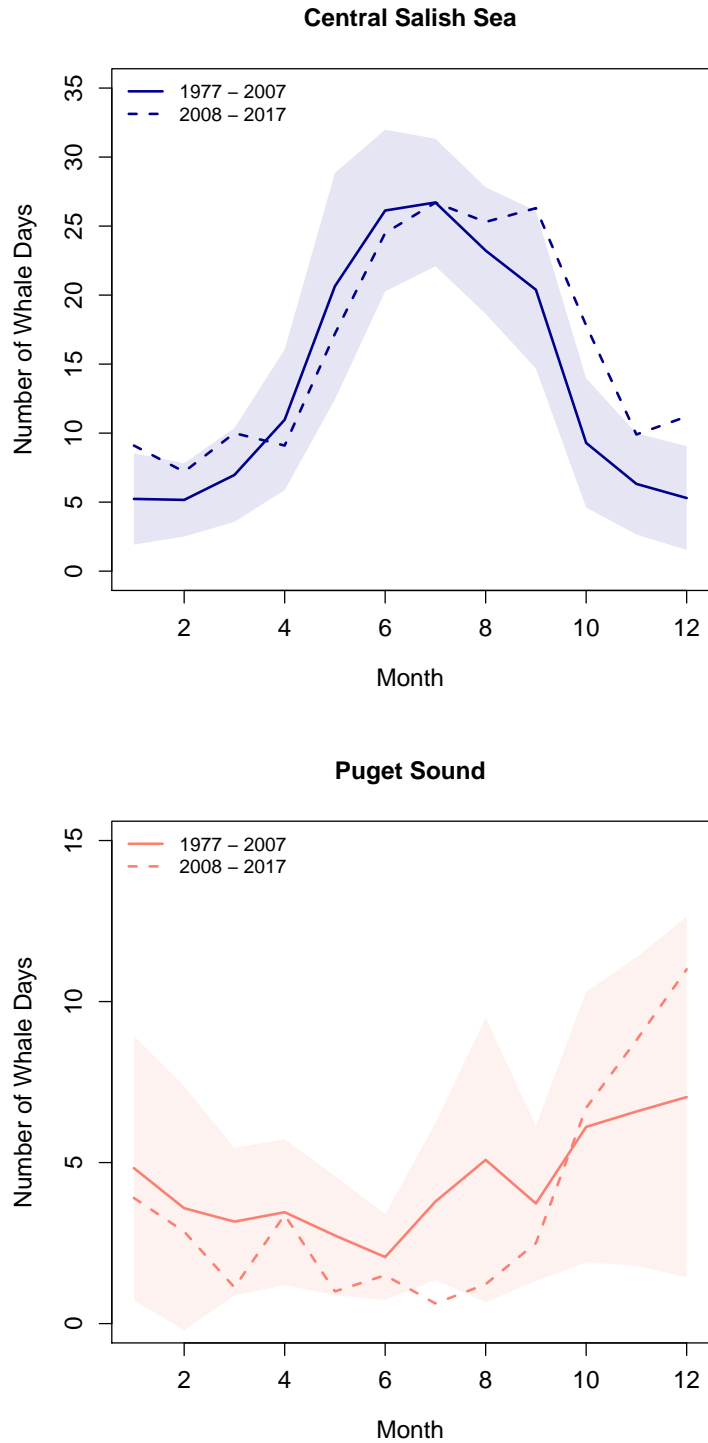


Figure 2: **Southern resident killer whale activity varies seasonally in the Central Salish Sea and Puget Sound proper** and this phenology has shifted later in recent years, particularly in the Central Salish Sea. Insets show linear trends in first-, peak-, and last- observation dates for J, K, and L pods, estimated from occupancy models. Error bars represent standard deviation.

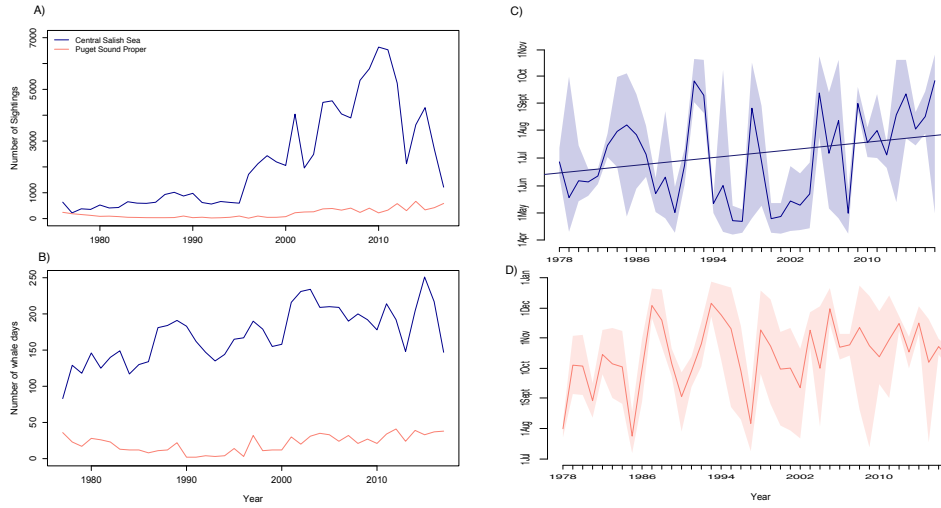


Figure 3: **Long-term trends differ from recent trends** for whale sightings (A), whale days (B), and peak occurrence probability in the Central Salish Sea (C) and Puget Sound proper(D). Occurrence probability for J pod is shown here; see Supplemental Materials for time series for K and L pods, as well as time series for other phenological estimates (i.e., first- and last- dates when occurrence probability is greater than 0.5). Shading represents 90% credible intervals.

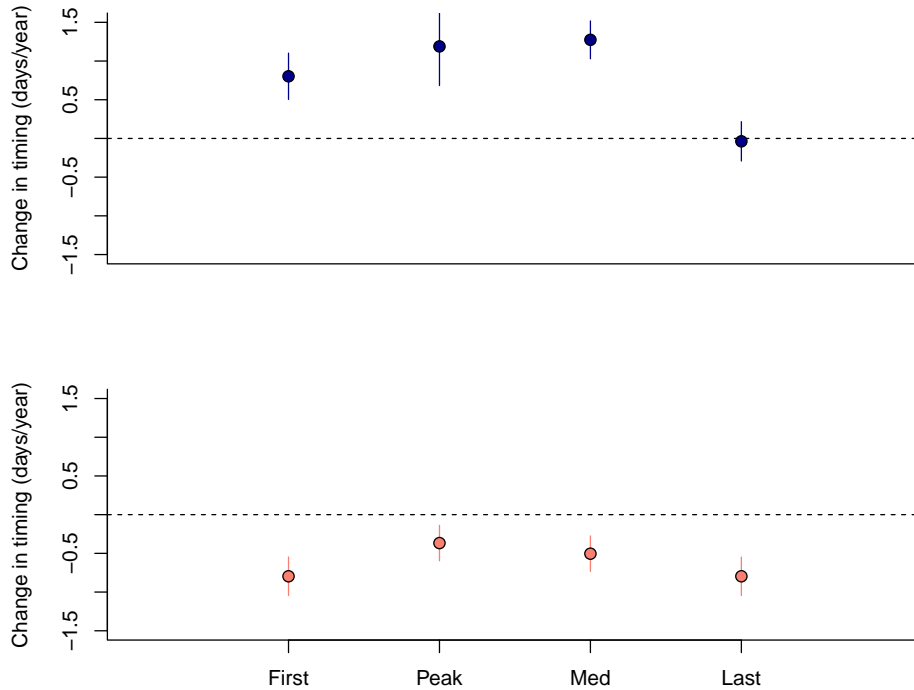


Figure 4: **Trends in first-, peak-, mid-, and last- observation dates for salmon** in the Fraser River Albion test fishery (upper panel), and across 17 different species/ivers in Puget Sound proper

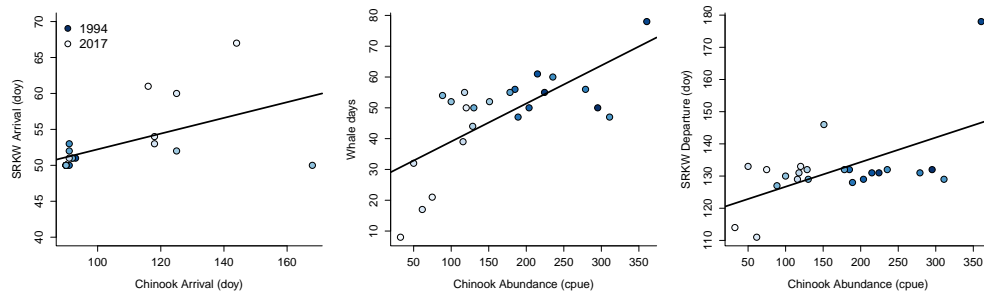


Figure 5: **SRKW phenology is related to estimated chinook phenology (A) and run size (B,C)**, for Lime Kiln State Park, a SRKW observation site in the central Salish Sea with a consistent data collection effort from 1994-2017 (from May through October,A). Chinook phenology and run size was estimated from the Fraser River Albion test fishery data. Phenology of the Central Salish Sea region as a whole appear to be less related to the patterns of this particular test fishery data, for many possible reasons (see Supplemental Materials for details).