1. Abstract

The timing, or phenology, of predator activity in relation to their prey is critical for survival and fitness, yet rarely quantified for marine species, even those of conservation concern. We use a large database of professional and citizen science observations analyzed with hierarchical spline occupancy models to quantify seasonal variation in occurrence of an endangered apex predator, the southern resident killer whale (SRKW, *Orcinus orca*), in inland waters of the Northeast Pacific Ocean. We find that timing of SRKW occurrence has shifted in their summer core habitat: the day of year of peak occurrence probability shifted later at rates of 1-5 days per year from 2001-2017 (resulting in shifts of 17-85 days across this17-year time period) in the Salish Sea. These shifts are consistent with shifts in their preferred prey, Chinook salmon (*Oncorhynchus tshawytscha*), as the relative number of fish returning to the Fraser River in the spring has declined compared to numbers returning in summer and fall. The shift in timing of fall/winter SRKW occurrence in Puget Sound proper, however, is not consistent with shifts in other prey populations (Chinook, coho [*O. kisutch*], chum [*O. keta*] salmon) returning to rivers in Puget Sound. Our findings demonstrate the complexity of consumer phenological responses and highlight gaps in our understanding of links between management actions that affect resource phenology and consequences for organisms relying on those resources.

2. Introduction

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

Despite its importance, phenology remains poorly understood in marine ecosystems, where it is far less studied than on land (Poloczanska et al. 2013). A recent, global 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), but the implications of these shifts are unclear. 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): the right amount of the resources available at the wrong time of year is no help to a consumer. Thus, management efforts that incorporate a rigorous understanding of phenology of focal species may be more effective, as they can lead to actions timed to coincide with (or avoid) biologically crucial events (Paton and Crouch, 2002; Morellato et al., 2016; Armstrong et al., 2016). A focus on timing may be especially important for threatened populations of large, highly mobile marine species, which may require management actions that are more finely tuned both spatially and temporally in order to avoid conflict with human activities (Lewison et al. 2015; Lascelles et al. 2014).

Despite its potential importance, phenology has not been quantitatively examined for southern resident killer whales (SRKWs, *Orcinus orca*), a large, highly mobile, and endangered marine population in the Northeast Pacific. SRKWs spend a portion of each year in the Salish Sea, the inland marine waters of Washington State, USA, and British Columbia, Canada (Fig. 1), but their geographic range varies seasonally: they have historically spent the most time in inland waters during the summer. During winter months their range expands to include coastal waters from Southeast Alaska to Central California (Balcomb III and Bigg, 1986; Krahn et al., 2005; Federal Register 2006). Like other populations of fish-eating ('resident') killer whales in the northeast Pacific Ocean, the primary prey of SRKWs during the spring and summer are salmon (*Oncorhynchus* species), especially Chinook salmon (*O. tshawytscha*; Hanson et al., 2010, 2021). The timing of SRKW movement is thought to be related to seasonal migrations of these prey. SRKWs use inland waters to hunt when salmon are aggregated and locally highly abundant, and have received widespread scientific and public attention in recent years as their numbers have declined (e.g., Lusseau et al., 2009; Fearnbach et al., 2018; Lundin et al., 2018; Ohlberger et al., 2019; Olson et al., 2018).

Insufficient prey availability is believed to be one of the primary threats to this population (Hanson et al., 2010; Ward et al., 2009; NMFS, 2008; Krahn et al., 2004; Krahn et al., 2002). This threat is exacerbated by the fact that SRKWs need to eat on a regular basis in order to maintain a positive energy balance (Noren 2011; Neill, Ylitalo, and West 2014), making it all the more important that the movements of these specialist predators are in sync with those of their prey. Salmon migrations to natal rivers occur seasonally, with patterns of presence and abundance varying among populations, species, and years, such that consumers (SRKWs, in this case) are likely to benefit from matched co-location to these prey in time and space (Armstrong et al. 2016; Deacy et al. 2017; 2018; Abrahms et al. 2020).

In recent decades, the abundance of salmon and timing of adult salmon migrations have shifted in western North America, with many populations declining and some adult returns occurring later (Morita, 2018; Weinheimer et al., 2017; Kovach et al., 2015; Satterthwaite et al., 2014; Reed et al., 2011; Ford et al., 2006; though patterns may differ among natural- versus hatchery-origin fish, (Austin, Essington, and Quinn 2021)). We would therefore expect SRKW phenology to have shifted during this time, if prey availability in inland waters is a primary driver of SRKW presence in inland waters (Fig. 2). If SRKW phenology has not shifted at a rate consistent with phenological shifts in their prey, the match-mismatch hypothesis would suggest that a mismatch could exacerbate the low prey availability they experience (Fig. 2). Alternatively, a mismatch between SRKWs and one of their prey populations may indicate that SRKWS are tracking an alternative prey source (other populations of Chinook salmon, or other prey species), or that

SRKW movements are tuned to other factors. Understanding these dynamics can inform the options for managing recovery for SRKWs, such as considering the migration timing of salmon stocks that are being enhanced to increase the SRKW prey base (SROTF, 2018) and the designation of critical habitat (cite something related to ESA Section 7).

Here, we seek to quantify seasonal variation in SRKW presence in the Salish Sea, the extent to which these seasonal patterns have shifted in recent decades, and whether potential shifts in SRKW presence may be related to changes in their prey. Specifically, we ask:

1. Has the timing of SRKW presence shifted in the Salish Sea?
2. If there have been phenological shifts in SRKW presence, do these shifts coincide with shifts in abundance and phenology of salmon?

We explore these questions first for one specific location in the Salish Sea (Lime Kiln Point State Park, Washington), where SRKWs have been well-studied with consistent effort by experienced observers over a relatively long time-period (May through August, 1994-present) and where a separate but relevant dataset allows peak migration phenology of their prey to be quantified over a similar time period and seasonal window. We also use a large, opportunistic database to increase the geographic scope of our analyses to include two broad regions over a somewhat shorter timeframe (2001-2017): the Central Salish Sea, which encompasses the summer core habitat of SRKWs (Federal Register, 2006), and Puget Sound proper, frequented most by SRKWs during the fall/winter season.

3. Materials and Methods

3.1 Focal species description

Southern resident killer whales often occur in the inland waters of Washington and southern British Columbia during the summer months (Olsen et al., 2018, Fig. 1). Southern residents are considered distinct from another partially sympatric population of fish-eating killer whales, known as northern resident killer whales, whose core distribution is centered around the north end of Vancouver Island, and from co-occurring 'transient' killer whales, which feed primarily on marine mammals (Ford et al., 1996; Krahn et al., 2005; Bigg, 1982). Southern residents experienced a 20% decline in the late 1990s, leading to their listing as endangered under the Canadian Species at Risk Act in 2003 and the US Endangered Species Act in 2005. The SRKW population currently stands at <75 individuals, and is composed of three pods, identified as J, K, and L, which are matrilineally related, cohesive, stable social groups. Individuals typically remain with their natal pods for all or most of their lives (Bigg et al., 1990). All three pods feed primarily on salmon, and insufficient prey availability is hypothesized to be a threat to the population (Krahn et al., 2002; Krahn et al., 2004; NMFS, 2008), along with chemical contamination, noise and disturbance from boat traffic, and small population size (e.g., Holt et al., 2009; Lusseau et al., 2009; Noren et al., 2009; Ward et al., 2009; Ford et al., 2009). Diet composition varies seasonally and across years, with Chinook salmon comprising the major prey in the spring and summer, an increased presence of Coho salmon (*O. kisutch*) in late summer and early fall, the addition of chum salmon (*O. keta*) in late fall and early winter, and other species in winter and early spring (Hanson et al., 2010, 2021; Ford et al., 2016).

3.2 Data

3.2.1 *Southern resident killer whale data*

To quantify changes in the timing of SRKW occurrence (phenology) in the inland waters of Washington state, USA, we first focus on SRKW timing from 1994 through 2017 at Lime Kiln Point State Park (henceforth "Lime Kiln"), which is located on the west side of San Juan Island (Fig. 1). We focus on this area and time period because SRKWs are systematically monitored and frequently observed from this location during the spring and summer months (Hauser et al., 2007). Data on the presence of whales in waters visible from the park viewing area were collected with consistent daily observer effort by experienced observers from May through early August over this two-decade period (Olson et al., 2018). Thus, an absence of observations from this location during this timeframe can be interpreted as a true absence of SRKWs at this local scale. In addition, this dataset offers a valuable opportunity to explore phenological patterns of both SRKWs and their prey because detailed data exist to quantify the timing of Fraser River Chinook salmon, which migrate through the area around Lime Kiln and make up a large proportion of the SRKW diet during the spring and summer months (Hanson et al., 2010, 2021).

We also quantified SRKW phenology across a wider geographic scope to understand if phenological patterns at one well-monitored site (Lime Kiln) match patterns across the broader Salish Sea region, where observation effort has been less consistent. For this broader analysis we used the Orca Master Database for killer whale sighting data (Olson et al., 2019,The Whale Museum, 2018), comprised of data from five main sources, including public reports to the Museum and other sightings networks (e.g., OrcaNetwork, http://www.orcanetwork.org/), commercial whale watch observations, Soundwatch boater education program observations, and multiple scientific survey efforts including data from satellite tracking units and hydrophones (see Olson et al., 2018 for details). Orca Master data extend as far back as 1948, but a dedicated effort to track SRKW presence in the region began in 1978 (Olson et al., 2018).

Despite the long time series of observations in the Orca Master dataset, it is important to understand the limitations of these data. The data are spatially biased (e.g., whale locations are unknown if they are not observed in the Salish Sea) and opportunistic in space and time. Additional samples in the dataset do not necessarily translate into more precise estimates of occurrence, because, for example, repeated sightings of the whales may contain redundant information. Nonetheless, these data comprise the most comprehensive set of SRKW observations. The data are thus uniquely poised to provide insight into changes in whale presence over time in this region, but careful interpretation is required since observer effort in this time series is not standardized, unlike the Lime Kiln observation data. For example, with increasing public awareness of SRKWs and the rise of social media, there has been a dramatic increase in reported sightings since 1978, especially following the establishment of internet-based reporting in 2000 (Olson et al., 2018). We therefore use pod-specific models to generate pseudo-absences (as described below, in section 3.3.2), and also focus our interpretation of trends in SRKW presence on the 2001-2017 time period. See *Effects of changes in effort on estimated phenological change* in the Supplemental Materials, especially Fig. S9, for additional details.

We used Orca Master sighting data to quantify SRKW presence in two core regions: the Central Salish Sea, used by SRKWs primarily from May through September, and Puget Sound proper, visited by SRKWs most commonly from September through January (Fig. 1). These seasonal definitions because are most aligned with mean SRKW seasonal patterns over time (Olson et al., 2018). Prior to fitting any models (see Section 3.x below), we used these raw data to quantify the number of "whale days" (i.e., days on which whales were observed) within a season and year for each region. This work is focused on the phenology of SRKWs, so we counted a whale day as a day on which one or more entries in the Orca Master database reported sighting "southern residents"' or J, K, and/or L pods specifically. Note that this approach differs from Olson et al. (2018), which included sightings of unidentified killer whale ecotypes in their analyses. Observation of any individual or group of whales within a pod counted as presence of that pod, with the exception of "L87," an individual that spent little time with his natal L pod following the death of his mother, and was instead seen more frequently with J- and K-pods. Observations of this individual alone were therefore not counted as presence of L pod in our analyses.

3.2.2 *Salmon data*

We quantified potential shifts in SRKW prey (i.e., adult salmon) peak migration timing coinciding with the timeframe and locations across which we summarize trends in SRKW timing. SRKWs feed primarily on Chinook salmon during the spring and summer season (encompassing 50-90% of their diet during this time), and approximately 80-90% of the Chinook salmon consumed by SRKWs during the months of May to September near San Juan Island (where Lime Kiln is located, Fig. 1) are from the Fraser River (Hanson et al., 2010, 2021). Many Chinook salmon returning to the Fraser River (across multiple populations with divergent migration timing) pass through the area where San Juan Island and Lime Kiln are located (WDFW, 2019; Parken, 2008). Thus, to quantify phenology of prey relevant to SRKW presence observed from Lime Kiln, we used adult salmon return data from the Albion Chinook salmon test fishery, located on the lower Fraser River at Albion, British Columbia, Canada, as an index of Fraser River Chinook (data available at https://www.pac.dfo-mpo.gc.ca/fm-gp/fraser/docs/commercial/albionchinook- quinnat-eng.html, Fig. 1). This test fishery is a consistent survey with standardized methodology and effort quantified, allowing for a robust index of the timing and abundance of Fraser River Chinook salmon migration during the spring and early summer (Parken et al., 2008, Fig. S1). Fraser River Chinook consist of multiple stocks that differ greatly in their life-histories (e.g., age, size, and run timing, Parken et al., 2008;

English et al., 2007). Changes in the realized phenology of Chinook salmon in the Lime Kiln area can therefore be due to both changes in the timing of individual stocks and/or changes in the relative abundance of stocks with different run phenologies. We made no attempt to distinguish between these two types of changes, but they may be important to SRKWs because the stocks can differ in nutritional value (O'Neill et al., 2014). We did not separate out distinct Chinook stocks within the Fraser River, as our goal was to quantify timing of peak abundance of all potential prey when SRKWs typically return to their summer core habitat (Fig. 1). We subtracted a lag of 10 days from the salmon phenology dates, to account for the time it takes salmon to swim between Lime Kiln the location of the Albion test fishery (Ayres et al., 2012). For the comparison to SRKW presence at Lime Kiln, we used only the data extending through August each year.

For the second analysis with wider geographic scope, ideally, we would compare SRKW timing to salmon timing in the same inland marine waters where SRKW sightings occurred. However, to our knowledge, spatially explicit daily or weekly data of salmon species presence or abundance across the full extent of these regions are not available. We therefore used data from watersheds where adult salmon arrive after passing through inland marine waters. We used two distinct datasets for salmon phenology. For the Central Salish Sea region, we used the Albion Chinook salmon test fishery data described above, but extending to the full season each year (i.e., through October instead of August). For Puget Sound proper, we used adult salmon stream count ('escapement') data for coho, chum, and Chinook salmon, available from the Washington Department of Fish and Wildlife (WDFW, https://wdfw.wa.gov/fishing/management/hatcheries/escapement). These daily or weekly data are available for 67 Puget Sound tributary streams since 1997 and include wild and hatchery counts. We selected sites located close to Puget Sound (i.e., within 25 km) with the greatest available data (i.e., time series across at least five years, with frequent monitoring during each year), and with relatively large run sizes (ranges of average counts from trap estimates were 1,400-30,000 for chum, 621-11,500 for coho, and 550-13,350 for Chinook). This filtering resulted in 13 runs, across three species and hatchery and/or wild salmon populations in 7 streams (Table S1). The particular runs we chose may not be widely represented in the SRKW fall/winter diet in Puget Sound proper, which has been sampled less than the spring/summer diet in the Central Salish Sea region, but they represent the best available data for adult salmon return phenology in Puget Sound tributaries. We include all three salmon species because the breadth of SRKW diet increases during the fall and winter months when SRKWs use Puget Sound Proper, and can include large proportions of chum and coho, in addition to Chinook salmon (Hanson et al., 2010, Ford et al., 2016). Note that these data were not used to estimate trends in abundance of SRKW prey or potential prey; rather, they were used to make inferences about potential shifts in salmon migration phenology within Puget Sound proper.

3.3 Analysis

We aimed to understand changes in phenology, which may be quantified in different ways (e.g., day of year of first occurrence, peak abundance or occurrence, last occurrence, CaraDonna, Iler, and Inouye 2014). Here, we estimated daily probability of occurrence for SRKWs and abundance for their prey, and use these estimates to identify three phenophases: first, peak, and last occurrence (Fig. S2). To quantify potential shifts in timing of each phenophase, we aggregate these estimates during different time periods (old versus recent, as in Figure 2). We also estimated linear trends in annual estimates of the three phenophases across the time series.

3.3.1 *Southern resident killer whales and their prey at Lime Kiln Point State Park*

To quantify the timing of SRKW presence at Lime Kiln, we fit hierarchical models in which the presence-absence of SRKWs (i.e., a Bernoulli response variable) was modeled as a semi-parametric, smooth function of day of year, using flexible thin-plate spline regression modelling, and year as a level. We used these models to estimate daily probability of occurrences for each year in the dataset (1994-2017), from which we derived annual dates of arrival, peak-occurrence probability, mean-occurrence probability, and total annual whale days (daily occurrence probabilities summed across all days in a year) for Lime Kiln Point State Park.

To estimate the phenology of Fraser River Chinook salmon, the main prey of SRKWs while in the waters near Lime Kiln, we fit a hierarchical thin-plate regression spline model to the Albion test fishery dataset (including returns through August annually), in which the response variable of catch per unit effort (CPUE, a continuous positive, normally distributed response variable). We adopted a similar model to SRKW phenology, modeling day of year with a smooth function, and year as a level. We used this model to estimate annual dates of arrival (defined as the first day of the year with CPUE greater than 0) and peak CPUE day of year. We also summed all daily CPUEs from April-August to use as an abundance index for early-season Fraser River Chinook salmon; this abundance index is consistent with some other indices for spring and summer Fraser River Chinook salmon escapement (Fig. S1, Parken et al., 2008; Chamberlain and Parken, 2012).

3.3.2 *Southern resident killer whales and salmon in the Central Salish Sea and Puget Sound Proper*

To compare the trends at Lime Kiln to trends in timing for SRKWs in the broader Central Salish Sea region and in Puget Sound proper, we analyzed the Orca Master sightings data to derive estimates of daily occurrence probabilities, summed annual modeled whale days (days with whales present), and arrival, departure, and peak-occurrence dates from 1978 through 2017 in two regions: the Central Salish Sea and Puget Sound proper (Fig. 1). We quantified pod-specific timing for J, K, and L pods using occupancy models, which estimate jointly presence and detection probability (the probability of detecting at least one individual present at a given site) by distinguishing true presence or absence from observed presence. Occupancy models are composed of a state sub-model, which is the model for the ecological process of true presence or absence, and an observation sub-model, which links the observations (in our model this was modelled as a binomially distributed variable, the number of sightings of the pod per day at a particular site out of the total number of sightings at the site that day) to the state model. We fit separate hierarchical occupancy models for each region (i.e., Central Salish Sea and Puget Sound proper) and season (spring/summer vs. fall/winter, since seasonal use varies by region) for each pod, accounting for non-independence of year with random effects, and extracted estimates of annual first, last, and peak occupancy dates with each model (see *Models* in the Supplemental Materials for details).

As a presence-only database, trends in the Orca Master dataset should be interpreted with care, since they could be due to shifts in effort (i.e., the number of total observations) as well as (or instead of) trends in SRKW presence (see *Effects of changes in effort on estimated phenological change* in the Supplemental Materials). For this reason, and because we know there has been a dramatic increase in reported whale sightings (Olson et al., 2018), we report all trends across two different durations: the full dataset (from 1978-2017) and recent years (2001-2017). We use 2001 as a cut-off, to avoid the sharp increase in sightings that occurred from 2000 to 2001 (Fig. S3-4), likely influenced by the onset of internet-based sightings platforms that began that year (Hauser et al., 2007; Olson et al., 2018).

To understand the phenology of likely prey in the Central Salish Sea, we used the above hierarchical thin-plate regression spline model fit to Albion test fishery data. For Puget Sound Proper we fit a separate model to each of the 13 Puget Sound runs to model daily salmon abundance indices for each year across the available time series. We then combined the Puget Sound runs and used a hierarchical linear model to identify trends over time in first, 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.

We assessed model performance through R_{hat} (which were close to 1) and high n_{eff}, as well as visual consideration of chain convergence and posteriors (Gelman et al., 2014). For additional analytical details, including model equations, see *Models* in the Supplemental Materials, and see Appendices for code. Throughout the manuscript, we present 75th percentile uncertainty intervals in all figures, 95th percentile uncertainty intervals parenthetically in the results, and include 50th, 75th, and 95th percentile uncertainty intervals in summary tables found in the Supplemental Materials.

4. Results

4.1 Southern resident killer whales and their prey at Lime Kiln Point State Park

Over the past quarter century (1994-2017), phenology of SRKWs shifted considerably Fig. 3at Lime Kiln (Figs. 3A, S6): across all pods together, the day of year corresponding to peak probability of occurrence has become later at a rate of 1.8 (95% CI: 0.70, 2.90, see also A) days per year. This corresponds to a shift of 43.3 (95% CI: 16.8, 69.6) days across the 24-year period of the data we analyzed. Comparison of an early time period to a more recent time period (based on dividing the time series in half) shows that the mean daily probability of occurrence for SRKWs (Fig. 3A) is ~20 days later in 2006-2017 compared to 1994-2005, on average, and that a reduced probability of occurrence early in the season was consistent across all three pods, especially for peak occurrence (Fig. S7). Using a breakpoint of 2006 or 2007 did not qualitatively alter results (Fig. S8). Arrival dates (for all pods together) delayed at a rate of 0.4 (95% CI: 0.8, 2.33) days per year , and departure dates did not change consistently in this dataset.

Over the same time period, the phenology of the predominant summer prey of SRKWs, adult Fraser River Chinook salmon, shifted in the same direction (Fig. 3B, 4B, Table S2): spring arrival dates delayed at a rate of 1.7 (95% CI :0.8, 2.6) days per year and peak abundance dates delayed at a rate of 2.7 (95% CI :0.84, 3.89) days per year. This corresponds to delays of 40.8 (95% CI: 19.2, 62.4) days for arrival date and 64.8 (95% CI: 20.16,93.36) days for peak abundance index date across the 24-year dataset. Comparing the1994-2005 and 2006-2017 periods, mean daily estimated CPUE for salmon shifted ~30 days later on average (Figs. 3B, S8). In addition to these changes in timing, annual sums of daily adult Chinook salmon CPUE, our index of Fraser River Chinook abundance, have declined over time (Fig. S5E).

Taken together, these results suggest that predator (SRKW) timing appears to be related to prey (Chinook salmon) timing and abundance at Lime Kiln. The later peak SRKW occurrence probability at Lime Kiln and the later dates of peak abundance of Fraser River Chinook salmon noted above are positively correlated (slope = 0.33, r-squared =0.20, p = 0.04; Fig. 3B). In addition, peak occurrence probability dates for SRKWs are earlier in years when Chinook salmon abundance indices are higher (slope = -0.13, r-squared = 0.31, p=0.007, Fig. 3C). Furthermore, the number of whale days has declined at Lime Kiln from 1994-2017 (Fig. S5), tracking declines in the Chinook salmon abundance index (from the Albion test fishery annual summed CPUE, slope = 0.05, r-squared = 0.31, p=0.009, Fig. S6). Whale days declined at a rate of -1.6 days per year (95% CI: -2.3, -0.9), resulting in 85% fewer observations in 2017 than in 1994. Since 2001, the decline is even steeper (-2.4 days per year, 95% CI: -3.5, -1.2, Fig. S5).

<u>4.2 Southern resident killer whales in the Central Salish Sea</u>

As at Lime Kiln Point State Park, in the Central Salish Sea there has been tremendous variability in the estimated peak occurrence probability for SRKWs (ranging from May 1 - September 1 in any specific year). However, despite this variability, it is clear that since 2001 SRKWs are more likely to be observed later in the year, particularly for J pod (Fig. 4A, 5A). In addition, although the predicted probability of occurrence for SRKWs in this region in spring (April through June) was near 1.0 from 2001-2008, since 2009 the expectation is much lower (less than 0.5 probability of occurrence in April) and does not approach 1.0 until nearly July (Fig. 4). In addition, the overall mean occurrence probability across the season has declined >25% for J-pod from 2001 through 2017 (from 0.85 to 0.64, Table S3). Trends across the full time-series (1978-2017) were also toward later peak occurrence probability, though they were less dramatic than since 2001 (e.g., 1.17 days per year delay from 1978-2017 versus 6.49 days per year delay from 2001-2017 for J-pod; Table S3). J-pod exhibits the most pronounced delays of the three pods; patterns for K- and L-pods vary (Figs. 5, S10, S11).

4.3 Southern resident killer whales and Chinook salmon in Puget Sound proper

As at Lime Kiln Point State Park and in the Central Salish Sea, in Puget Sound proper the day of first SRKW occurrence has delayed since 2001for all three pods (Fig. 5C). Trends in peak and departure dates vary across pods: for example, peak and departure dates are delaying for K -pod. However, peak occurrence probability date has not shifted consistently for J- and L-pods (Fig. 5C). As in the Central Salish Sea, the day of peak occurrence is variable, but ranges over a two-month period (from late September to early December) rather than a four-month period (Fig. 5C,D). Mean occurrence probability has declined in Puget Sound proper since 2001, by ~25% (Fig. 5C bottom right), but uncertainty intervals are wide for the period from 2001-2008, especially during the early part of the season (Table S3). Across the full dataset (1978-2017), the trend has been toward later peak occurrence for all three pods (delaying at rates of 1.13 (95% CI: 0.33, 1.93), 1.75 (95% CI: 0.76, 2.62), and 1.07 (95% CI: 0.41,1.65), days per year for J, K, and L pods, respectively (Table S3). These trends in SKRW occurrence are opposite those of adult salmon returns in Puget Sound: we find a shift toward slightly earlier returns (advancing rates of 0.4 to 0.7 days per year, on average across all 13 runs; Fig. 5D)

5. Discussion

Shifts in the timing of biological events have been identified in diverse species and ecosystems around the world (Poloczanska et al., 2013). However, the importance and management implications of phenological shifts in consumers and their prey, as well as the potential for match-mismatch dynamics, remain poorly understood (Visser and Gienapp 2019; Kharouba et al. 2018; Morellato et al. 2016; Paton and Crouch III 2002). Developing management plans in response to phenological shifts is important, though challenging, especially in threatened and endangered species, for which there is often a paucity of data and a greater emphasis on population-level studies, rather than community or ecosystem-level research (Carroll et al., 2017; Gilman et al., 2017; Tylianakis et al., 2008). Failure to apply the right management measure at the right time-- such as a fishery closure to avoid harvest and consumption of species containing toxins produced by algal blooms (Cavole et al. 2016)– can lead to undesirable social outcomes. Here we use two extensive datasets, including standardized data as well as opportunistic presence-only data analyzed with hierarchical occupancy models, to show that the timing of SRKW presence in the Salish Sea has shifted over the past 40 years. This suggests that management developed around this species' historic spatiotemporal patterns may not be consistent with present day patterns. Furthermore, we demonstrate that, in recent years, the occurrence of SRKWs peaks later in the Central Salish Sea, a change consistent with observed changes in the timing of peak availability of their favored prey, Chinook salmon (Fig. 3).

Our findings in the Central Salish Sea align with accumulating evidence that resource tracking can drive timing of consumer movement. Both proximate cues and long-term memory are thought to drive migrations of consumers across terrestrial and marine taxa (Abrahms et al. 2020; 2019; Aikens et al. 2017; Armstrong et al. 2016). Consumer movement may track resources so that consumers can derive an energetic benefit, implying that movement toward a location occurs because resources are more readily available there than elsewhere. In this study, we observed shifts in timing of SRKW presence at a single consistently-observed site (Lime Kiln; Fig. 3), where these shifts were corelated with concurrent delays in the peak timing of their preferred resource, Fraser River Chinook salmon (Hanson et al. 2010), which return annually to inland waters of the Salish Sea during their spawning migrations. Furthermore, across the broader Central Salish Sea region, the magnitude and direction of shifts toward later arrival and peak occurrence by SRKWs (J- and K- pods, specifically) corresponds to later arrival of Fraser River Chinook salmon (Fig. 5). While future work must disentangle the many potential factors influencing shifts in the timing of occurrence of SRKWs in inland waters, these findings imply that the relative benefits for SRKWs early in the year are not as great now as they once were.

The evidence provided here is thus consistent with the idea that SRKWs have tracked phenological shifts in salmon prey resources. This may not be surprising, given the numerous other observations of consumer phenological tracking and even altering the spatiotemporal patterns of resource waves (Abrahms et al., 2019; Geremia et al., 2019; Aikens et al., 2017; Armstrong et al., 2016). On its face, this might appear to allay concerns over phenological mismatch with climate change (Kharouba et al., 2018, Sergeant et al., 2015). However, changes to prey phenology could nonetheless contribute to the prey shortages experienced by SRKWs. For example, in our study the delay in the peak abundance timing of Fraser River Chinook is driven primarily by a collapse of spring Fraser River Chinook populations (Fig. 3, Riddell et al., 2013, Pacific Salmon Commission 2019), rather than from all populations in the Fraser River shifting their migration timing later. (In fact, river entry timing of many individual runs shifted earlier from the 1982 to 2004, English et al., 2007). If reductions continue in the spring Fraser River Chinook run, this may lead to a narrowing in the duration of Fraser River runs and a reduction in phenological diversity, as is occurring in other locations and life stages of Chinook salmon in the region (e.g., Nelson et al. 2019). In turn, reductions in prey phenological diversity could enhance the probability that SRKW individuals experience extended periods without encountering prey, prevent them from maintaining a positive energy balance, and have strong, negative effects on these consumers (Armstrong et al., 2016).

In contrast to the Central Salish Sea, our findings in Puget Sound proper highlight that resource timing may not be the sole driver of consumer phenology. In Puget Sound proper SRKW presence does not appear to be shifting coincidently with shifts in salmon migration timing (Fig. 5). Instead, contemporary phenology of this highly mobile species may be driven by environmental cues that do not correspond to the resource upon which they depend, even if historical consumer phenology did follow resource-based cues (e.g., Both et al., 2009; Chmura et al., 2019). Human activity, such as vessel traffic and noise, can affect movement and behavior of SRKWs and other marine animals (Ivanova et al., 2019, Noren et al., 2009, Holt et al., 2009; Lusseau et al., 2009). Social cues, learning, and memory can also affect migratory behavior and timing (Samplonius and Both, 2017; Jesmer et al., 2018; Abrahms et al., 2019, Brent et al. 2015). For example, it is possible that SRKWs enter inland waters following a resource wave of Chinook salmon in the spring and summer; they may then follow habitual routes into Puget Sound proper to scout for other prey, rather than tracking a particular resource.

Predator-prey phenological relationships are important considerations in conservation and management actions related to SRKWs and many other species. Assessment of phenological variation is rarely incorporated into management, even though the timing of consumer-resource overlap and disturbances have critical implications for population dynamics and viability (Armstrong et al., 2016; Morellato et al., 2016, Furey et al., 2011). We suggest that explicitly incorporating phenological assessments may benefit species-specific management (e.g., examination of changes in critical habitat over time for endangered SRKWs, under ESA Section 7) as well as broader efforts such as ecosystem-based fisheries management, which strives to account for species interactions, ecosystem-scale forcing, protected species tradeoffs, and other dynamics as essential components of sustainable fisheries practices (Pikitch et al., 2004; Schindler et al., 2013, Link and Browman 2017). For example, in the case of SRKWs, knowledge of the timing of their movements to inland waters could be used to develop rolling, in-season, salmon fisheries harvest reductions. Our analysis implies that such conservation measures will be more effective if applied later in the year, when SRKWs are most likely to peak in occurrence in the Central Salish Sea, than would have been sensible two decades ago, when their occurrence probability would have been more likely to peak earlier.

Our work underscores challenges associated with conservation of predators such as SRKWs. Although reduced prey is a clear threat facing this endangered population, ameliorating the threat by increasing salmon abundance is not straightforward. On the one hand, detailed knowledge of predator and prey co-occurrence in space and time, such as the relationships we quantify here between salmon and SRKW phenology, may provide a means of focusing recommended management efforts to enhance salmon abundance in the region, through actions such as hatchery production, restrictions on salmon harvest, removal of dams on salmon rivers, restoration of salmon habitat, and predator culling (SROTF 2018, Berdahl et al. 2017). On the other hand, the lack of correspondence between SRKW and Puget Sound salmon phenology highlights gaps in our mechanistic understanding of links between the timing of a management action and its consequences for the timing of ecological interactions. Salmon hatchery programs have been utilized in the Pacific Northwest for the dual purposes of enhancing production for fisheries, and as a conservation tool. Previous research has highlighted the phenological differences between hatchery and wild Chinook salmon (Austin et al. 2020), but the impacts of changing Chinook hatchery production on the total temporal distribution of prey for SRKWs is not understood. If salmon enhancement itself is successful, translating that success to SRKW recovery will likely depend on increased understanding of SRKW phenology across annual movement and feeding cycles, so that pod-specific forecasts can be developed and used to tailor the enhancement strategy to the characteristics driving spatial and temporal variability of each SRKW pod.

Regardless of the conservation approaches implemented, attention to factors beyond the Salish Sea is a critical component of effective recovery actions (Levin, Howe, and Robertson 2020). In this paper we used the largest available database on SRKW presence. Despite possible shortcomings in these data, there is a great need for presenting and analyzing them, given the large amount of resources proposed to be spent on SRKW recovery and salmon enhancement (>$1billion, https://www.governor.wa.gov/sites/default/files/Final%20Draft%20LSRD%20Report.pdf). Further, the data are substantial enough to fit our models and estimate the parameters of interest. That said, changes in the timing of availability of the preferred prey of SRKWs outside of the Salish Sea are less well-understood but no doubt affect shifts observed within the Salish Sea. Across fine to broad scales, incorporating a perspective focused on timing of biological interactions, in addition to one focused on the abundance of interacting species, may enhance effectiveness of efforts to conserve and manage consumers and resources in the face of global change.

6. References

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7. Figures

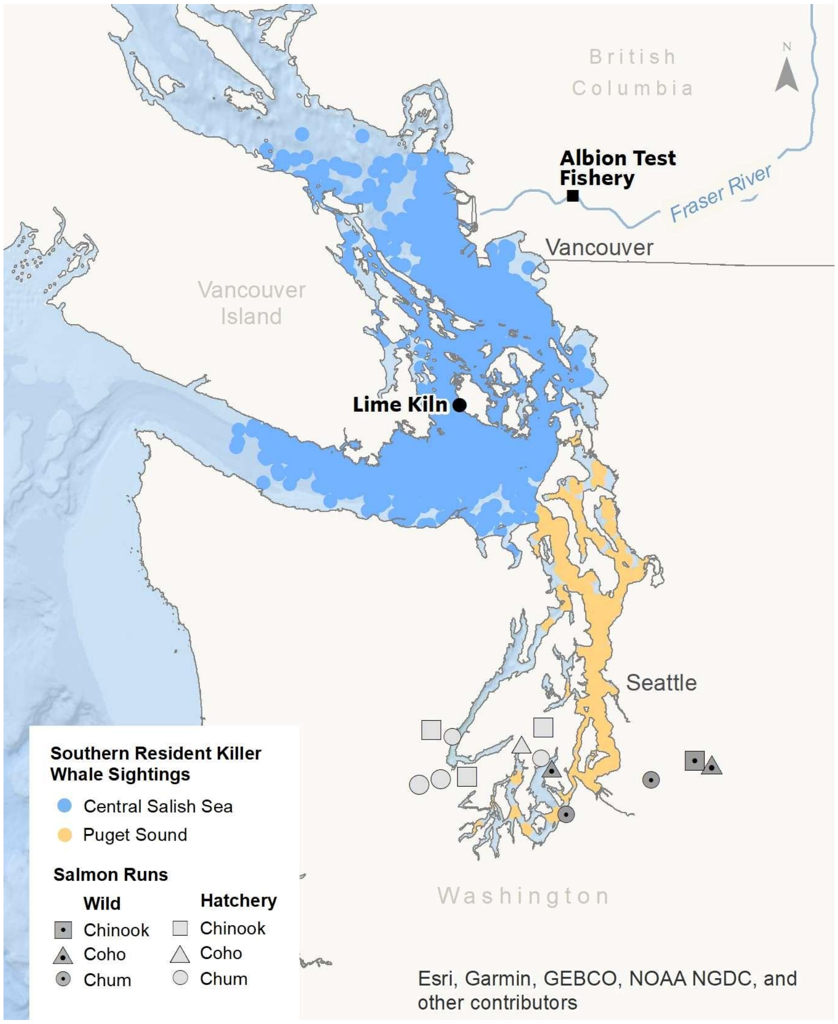

Fig. 1: Southern resident killer whale (SRKW) presence varies across two broad regions: the Central Salish Sea (blue dots), which includes their core summer habitat, and Puget Sound proper (yellow dots), where SRKWs frequent most often in the fall and winter (sighting data from the OrcaMaster database, from 1978-2017) Lime Kiln Point State Park is the location of consistent monitoring and data-collection on SRKW presence from May through August. Data from the Albion Test Fishery, which is conducted in the Fraser River in British Columbia and

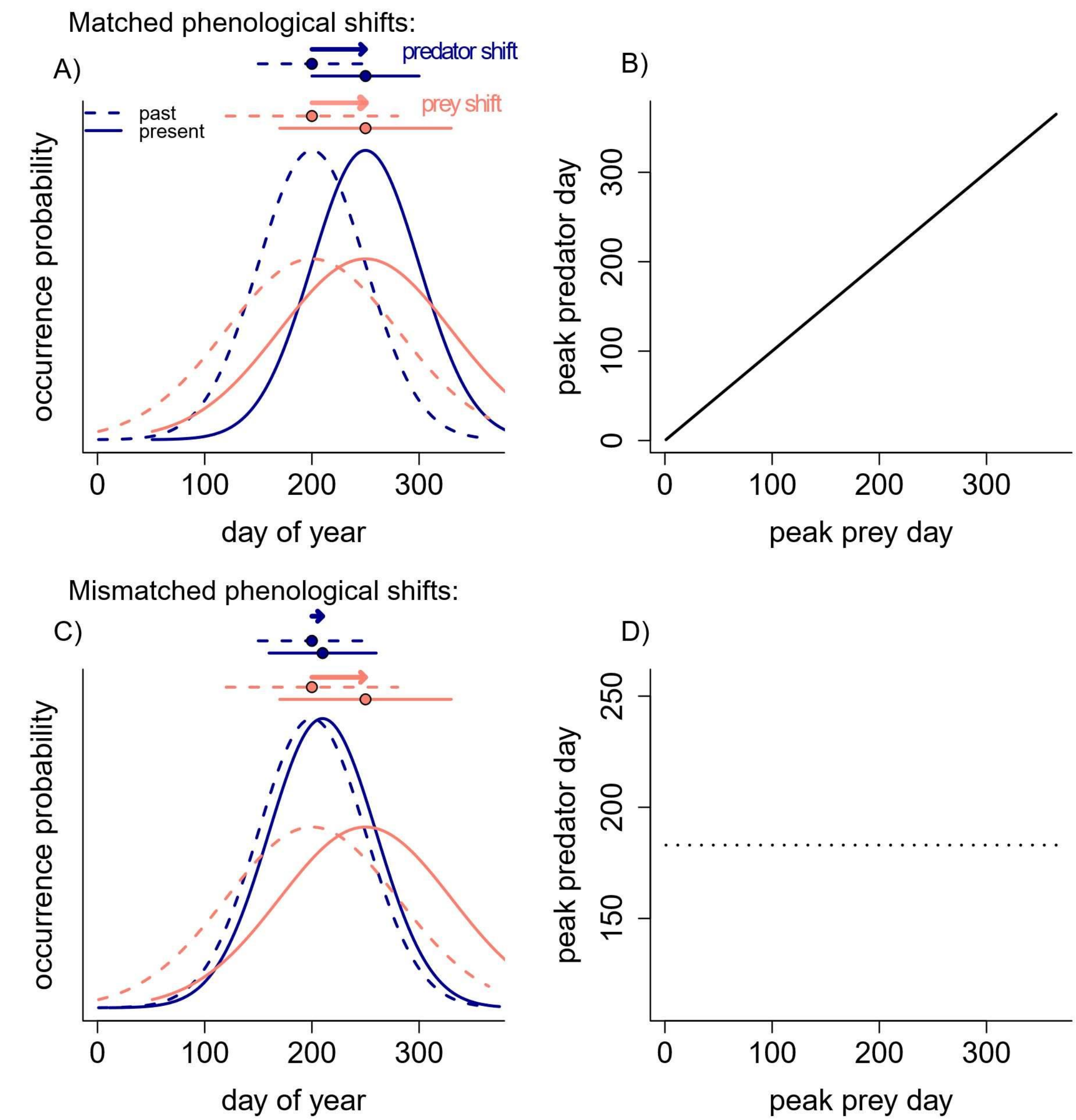

Fig. 2. Conceptual schematic for hypothesized shifts in timing of predators and their prey. Predator, such as southern resident killer whales (SRKWs), phenology may be shifting over time, in concert with prey, such as salmon (‘matched phenological shifts’), A), such that predator timing is correlated with prey timing across years (i.e., a year for early peak abundance, or occurrence probability of prey, is an early year for peak occurrence of predators, B). Points show the day of peak abundance or occurrence probability whereas curves show the seasonal pattern. If prey phenology is shifting, but predator phenology is not (or is not shifting at the same rate) this may lead to mismatches in the timing of predators and their prey (‘mismatched phenological shifts’) C). Mismatched phenology could reduce realized prey availability to predators, even if prey abundance is unchanged, and predator timing would be poorly correlated with prey timing across years in this case, D).

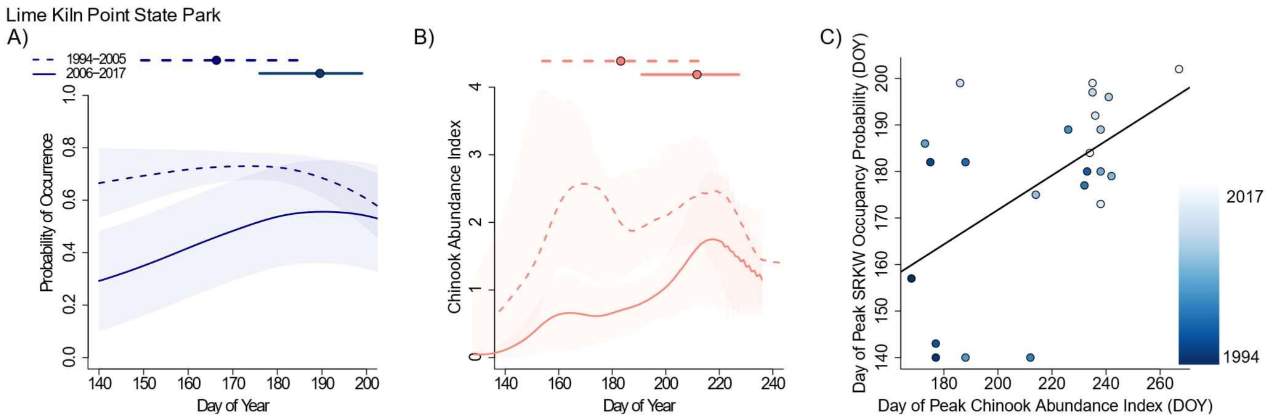

Fig. 3: Southern resident killer whale phenology has shifted, in concert with shifts in Fraser River Chinook Salmon at Lime Kiln Point State Park, one site with consistent observations from May 1 (day of year 140) through August 1 (day of year 215) in the Central Salish Sea. Timing of SRKWs (A) and Fraser River Chinook salmon (B) has delayed in recent (solid lines) compared with earlier (dashed lines) years, with day of year of peak occupancy probability shifting from a mean of 168 from 1994-2005 to 192 from 2005-2017 (points in A), and day of year of peak abundance index shifting from a mean of 191 from 1994-2005 to 220 from 2005-2017 (points in B). Shading and error bars show 75% uncertainty intervals. Patterns here are for all SRKW pods together; see Supplemental Materials for each pod separately (Fig. S7). Fraser River Chinook salmon travel past the area around Lime Kiln Point State Park earlier in their migration route than the location where data were collected (the Albion Test Fishery, which encompasses multiple distinct runs), so we have added a lag of 10 days to the salmon phenology (Ayres et al., 2012). Changing the breakpoint to 2007 or 2005 did not qualitatively alter results (Fig. S8). Dates of peak probability of occurrence for SRKWs are positively associated with dates of peak abundance index for Chinook (C). (Extending the seasonal window to October to calculate CPUE did not qualitatively alter patterns shown here.)

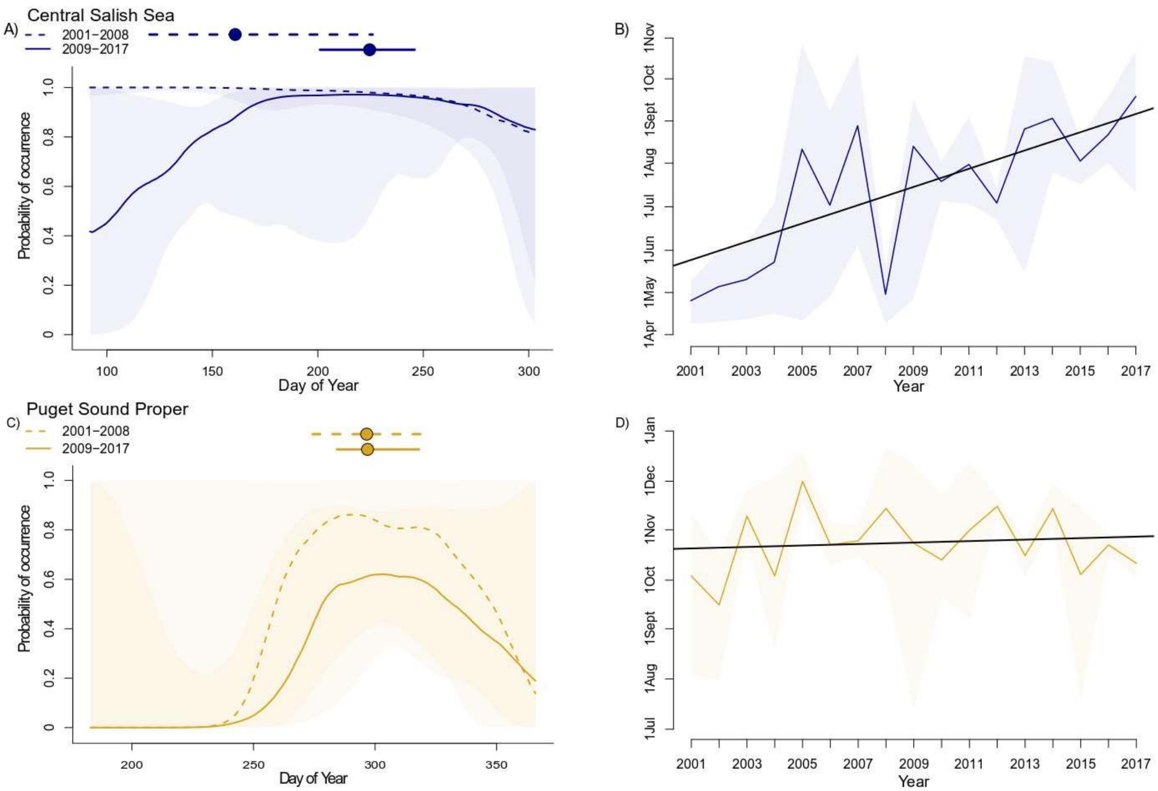

Fig. 4: Southern resident killer whale (J-pod) presence varies seasonally in the Central Salish Sea (A) and Puget Sound proper (C) and peak probability of occurrence has shifted later in recent years in the Central Salish Sea (B) but not in Puget Sound proper (D). The shift toward later arrival in the Central Salish Sea is evident in the estimated probabilities of occurrence from the occupancy model for J-pod, with mean day of year of peak occurrence probability shifting from 171 from 2001-2008 to 222 from 2009-2017 (points in A, lines around points show 75% uncertainty), as well as the linear trend in peak occurrence probability from 2001-2017 (B). Shading around lines represents 75% uncertainty intervals. Estimated probabilities of occurrences for K- and L-pods can be found in Figs. S10 & S11.

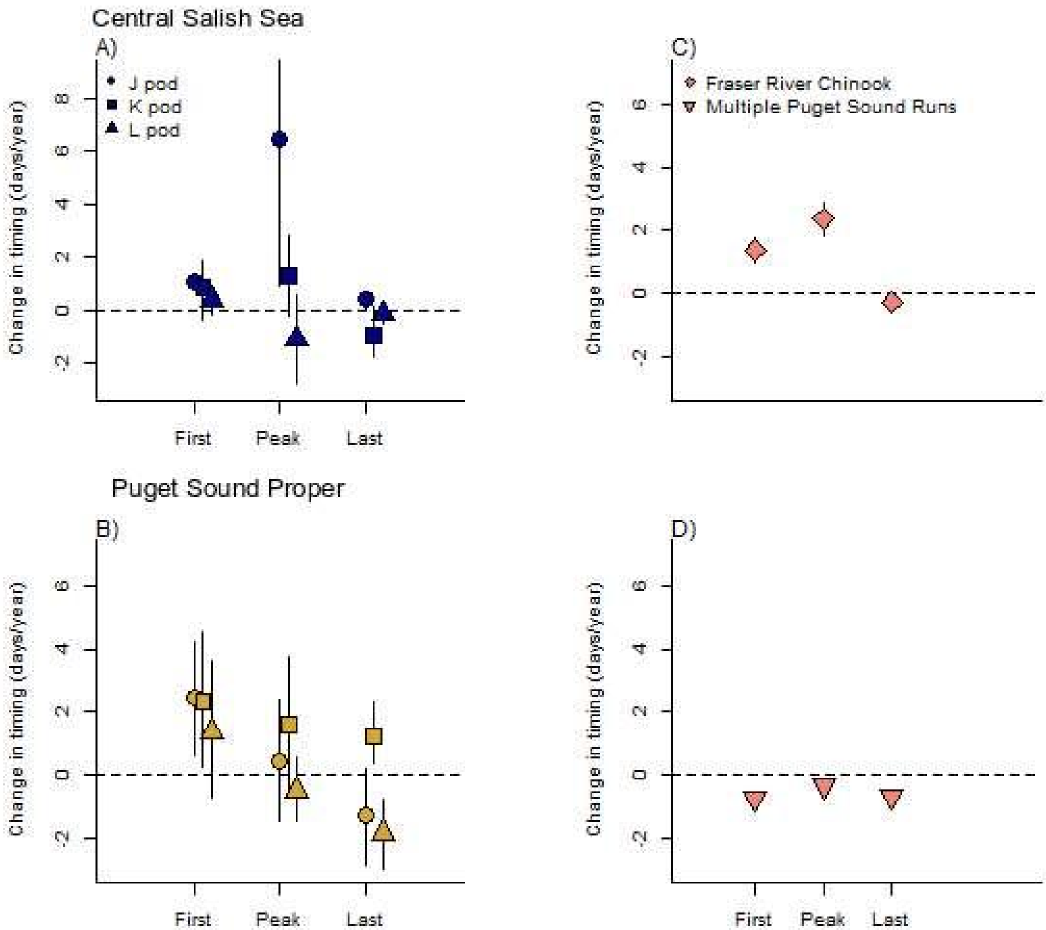

Fig. 5: Trends in SRKW (A,B) and salmon (C,D) phenology in the Central Salish Sea (upper panels) and Puget Sound proper (lower panels) from 2001 through 2017. SRKW shifts are summarized from linear models fit to estimates of day of year of first day of likely occurrence (probability of occurrence >0.5), peak probability of occurrence, and last day of likely occurrence from pod-specific occupancy models in each region. Salmon shifts are from linear models fit to Fraser River Chinook estimates from the Albion test fishery for the Central Salish Sea, and from a hierarchical linear model fit to escapement data across 13 distinct groups (including three species of wild and hatchery origin across 7 different streams) in for Puget Sound proper. Error bars show 75% uncertainty intervals (95% uncertainty intervals are in Table S3).