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Shifting phenology of an endangered apex predator mirrors changes in its favored prey

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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 crowd-sourced 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 within the central Salish Sea: the day of year of peak occurrence probability shifted later at rates of 1–5 d yr^{-1} over 2001–2017 (resulting in shifts of 17–85 d across this 17 yr time period). These shifts are consistent with shifts in their preferred prey, Fraser River Chinook salmon *Oncorhynchus tshawytscha*, as the relative number of fish returning to spawn in the spring has declined compared to numbers returning in summer and fall. The shift in timing of fall/winter SRKW occurrence outside the summer core habitat, however, is not consistent with shifts in other prey populations (Chinook, coho *Oncorhynchus kisutch*, chum *Oncorhynchus keta* salmon) returning to nearby rivers. 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.

KEY WORDS: Trophic mismatch · Global change · Phenology · Salmon · Southern resident killer whale · Orca · *Orcinus orca*

1. INTRODUCTION

Phenology, or the timing of biological processes (e.g. migration, growth, reproduction), can have dramatic implications for individual fitness and population success (Chuine 2010, Lane et al. 2012). Consumer phenology that is out of step with timing of its resources can cause increased mortality and reduced reproductive success (Post & Forchhammer 2008), problems that may jeopardize recovery of threatened or endangered species. The critical nature of these 'matches' or 'mismatches,' originally described for fish and zooplankton (Hjort 1914, Cushing 1990), has received renewed scientific interest as phenological shifts have been increasingly observed in conjunction with recent climate change (e.g. Durant et al. 2007, Poloczanska et al. 2013, Kharouba et al. 2018).

Despite its importance, phenology in marine ecosystems remains poorly understood, compared to phenology in terrestrial ecosystems (Poloczanska et al. 2013). A global meta-analysis found that recent shifts in marine phenology are at least as dramatic as those observed in terrestrial systems (e.g. −4.4 ± 0.7 d $decade^{-1}$ across diverse species from algae

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and zooplankton to seabirds and fish, Poloczanska et al. 2013), but the implications of these shifts are unclear. In ecosystems where shifts in the timing of biological processes for consumer populations are well understood, the causes range from abiotic influences on availability of forage resources to human disruption of migratory routes. Despite the importance of phenology to population dynamics (Hipfner 2008), the abundance of resources, not their timing, is often a focus of natural resource management. Management efforts that also incorporate a rigorous understanding of phenology may be more effective, as they can lead to actions timed to coincide with (or avoid) biologically crucial events (Paton & Crouch 2002, Armstrong et al. 2016, Morellato et al. 2016). A focus on timing may be especially important for threatened populations of large, highly mobile marine species with specialized diets, as they may rely on different seasonal resource bases spread across wide geographic areas. Conserving these species may require management actions and recovery strategies that are more finely tuned both spatially and temporally in order to maximize effectiveness while avoiding conflict with human activities (Lascelles et al. 2014, Lewison et al. 2015).

These management and recovery challenges are exemplified in southern resident killer whales (SRKWs) *Orcinus orca*, an endangered population in the northeast Pacific Ocean, for which phenology has not been rigorously quantitatively examined. Southern residents are considered distinct from other fish-eating 'resident' killer whales (northern resident killer whales, whose core distribution is further north) and from co-occurring 'transient' killer whales, which feed primarily on marine mammals (Ford et al. 1996, Krahn et al. 2007). The geographic range of SRKWs varies seasonally (see Fig. 1) and the timing of their movement is likely related to migrations of their predominant prey, salmon *Oncorhynchus* spp., especially Chinook salmon *O. tshawytscha* (Hanson et al. 2010, 2021). SRKWs use inland waters to hunt when salmon are aggregated and locally highly abundant, and insufficient prey availability is believed to be a primary threat to this population (NMFS 2008, Ward et al. 2009, Hanson et al. 2010). This threat is exacerbated by the fact that, as large mammals, SRKWs need to eat on a regular basis in order to maintain a positive energy balance (Noren 2011). Further, the large spatial and temporal variation in salmon abundance, driven by migrations to natal rivers, make it particularly critical for SRKWs to align their movements with those of their prey (i.e. resource tracking, Armstrong et al. 2016, Deacy et al. 2018, Abrahms et al. 2021).

In recent decades, the abundance and timing of migrating adult salmon have shifted in western North America, with many populations declining and some adult returns occurring later due to climate change, hatchery and fishing practices, or other ecosystem changes (e.g. Ford et al. 2006, Satterthwaite et al. 2014, Kovach et al. 2015, Morita 2019). We would therefore expect SRKW phenology to have shifted during this time, if prey availability is a primary driver of SRKW presence in a given region (see Fig. 2). If SRKW phenology has not shifted at a rate consistent with phenological shifts in their prey, the resulting mismatch could exacerbate their low prey availability (see Fig. 2 and Hjort 1914, Cushing 1990). Understanding these dynamics can inform 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 and the designation of critical habitat (SROTF 2019).

Here, we seek to quantify seasonal variation in SRKW presence in the Salish Sea (see Fig. 1), 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 between 1994 and 2017? (2) How does SRKW phenology coincide with recent shifts in abundance and phenology of salmon?

2. MATERIALS AND METHODS

2.1. Focal species description

SRKWs have historically occurred regularly in the inland marine waters of Washington state (USA) and southern British Columbia (Canada) during the summer months (Fig. 1 and Olson et al. 2018). During winter months, their range expands to include coastal waters from southeast Alaska to central California (Krahn et al. 2007, Federal Register 2006). SRKW population size declined by ~20% in the late 1990s (from 98 to 80 individuals), 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 has continued to decline and currently stands at approximately 75 individuals. The population consists of 3 pods, identified as J, K, and L, which are matrilineally related, cohesive, stable social groups. Individuals typically

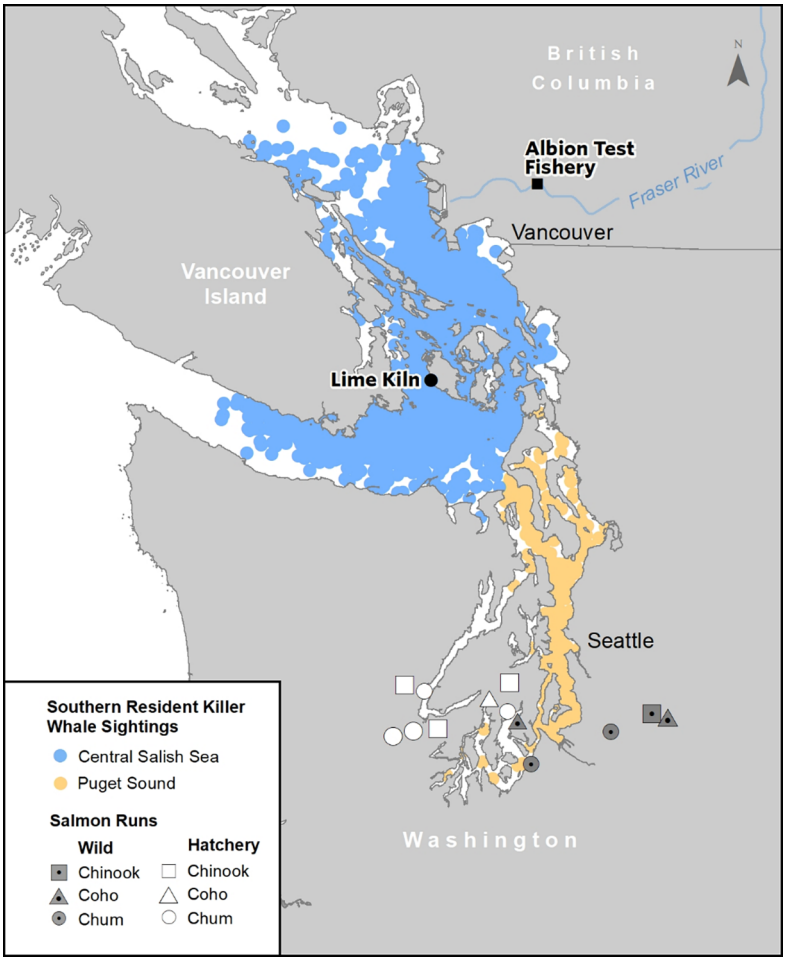

Fig. 1. Southern resident killer whale (SRKW) presence varies across 2 broad regions: central Salish Sea, which includes the population's core summer habitat, and Puget Sound proper, where SRKWs frequent most often in fall and winter (sightings data from Orca Master database, 1978–2017). Lime Kiln Point State Park is the location of consistent monitoring and data collection on SRKW presence from May through August. Data from the Albion test fishery (Fraser River, British Columbia) are used here to quantify phenology of SRKW prey in the central Salish Sea. Data from 13 salmon runs, across 3 species and hatchery and/or wild salmon populations in 7 streams (Table S2), are used to quantify shifts in potential prey phenology in Puget Sound

remain with their natal pods for all or most of their lives (Bigg et al. 1990). All 3 pods feed primarily on salmon, and insufficient prey availability, which has been linked to survival and fecundity rates, may be partially responsible for the population decline, along with chemical contamination, noise and disturbance from boat traffic, and inbreeding depression due to small population size (e.g. NMFS 2008, Ford 2009, Lusseau et al. 2009, Noren et al. 2009, Ward et al. 2009, Ford et al. 2018). 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 *Oncorhynchus kisutch* in late summer and early fall, the addition of chum salmon *O. keta* in late fall and early winter, and other salmon and non-salmonid fish species in winter and early spring (Hanson et al. 2010, 2021, Ford et al. 2016). Chinook salmon originating from southern British Columbia river systems (especially the Fraser River) are particularly important spring and summer prey for SRKWs in the Salish Sea (Hanson et al. 2010, 2021).

2.2. Overview of phenology and focal response variables

Here, we estimated daily probability of occurrence for SRKWs and daily abundance of salmon, and used these estimates to identify 3 phenophases: 'first,' 'peak,' and 'last' likely occurrence (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n048p211_supp.pdf). We use multiple phenophases because changes in phenology can be quantified in different ways that may have varying patterns over time (e.g. day of year of first occurrence vs. peak abundance or last occurrence, CaraDonna et al. 2014). To quantify potential shifts in timing of each phenophase, we aggregated these estimates during different time periods (more distant vs. more recent past, as in Fig. 2) and quantified linear trends in annual estimates of the 3 phenophases across the time series. Because the overall occurrence and abundance of SRKWs and salmon is also of interest from a conservation and management perspective, and changes in these values may influence changes in phenology (e.g. differences in the total amount of salmon prey available to SRKWs may change the timing of peak occurrence of SRKWs, even if the timing of prey availability remains constant), we also summarized the total days in inland waters for SRKWs annually and developed an annual abundance index for salmon. We used modeled estimates, rather than raw data, because we wished to quantify and statistically account for among-year variation in abundance and observation effort that can affect phenology estimates (Strebel et al. 2014).

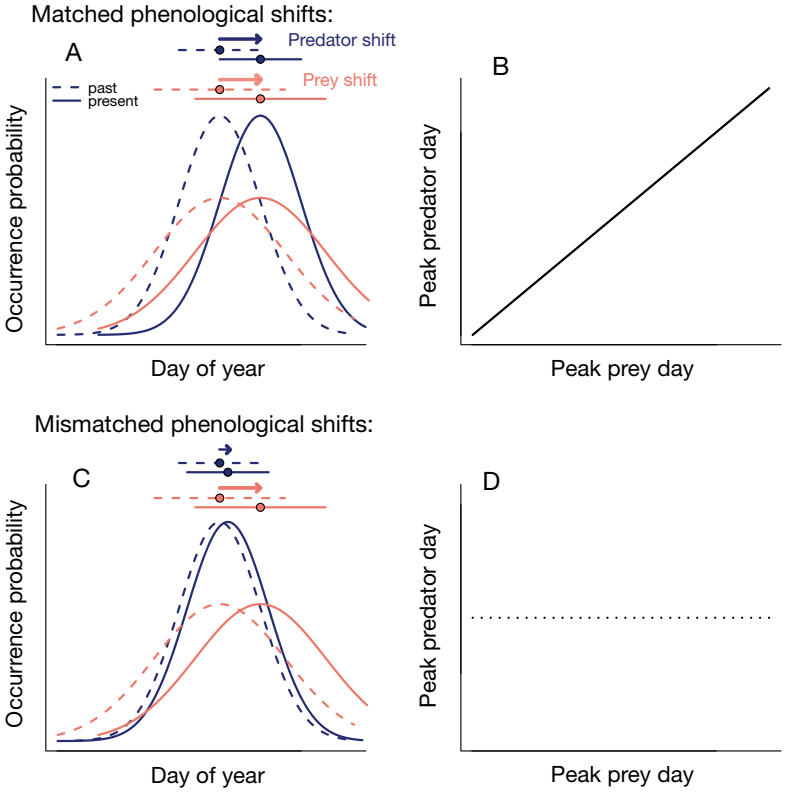

Fig. 2. Conceptual schematic for hypothesized phenological shifts in timing of predators in response to their prey. (A) Phenology of predators, such as southern resident killer whales, may be shifting over time, in concert with prey, such as salmon ('matched phenological shifts'), such that (B) predator 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). (C) If prey phenology is shifting, but predator phenology is not (or not at the same rate), this may lead to mismatches in the timing of predators and their prey ('mismatched phenological shifts'); (D) this 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. In (A) and (C), points are day of peak abundance or occurrence probability; curves are the seasonal pattern

2.3. Data

2.3.1. SRKW data

We analyzed 2 datasets of SRKWs in the Salish Sea: a local-scale dataset from a single, consistently monitored site, and a broader regional dataset that includes crowd-sourced observations. The localized dataset tracks occurrences of SRKWs from 1994 to 2017 at Lime Kiln Point State Park (henceforth 'Lime Kiln'), located on the west side of San Juan Island in the central Salish Sea (Fig. 1). SRKWs are known to feed at this site during the spring and summer months (Lusseau et al. 2009) and have been systematically monitored here since 1994 (Hauser et al. 2007). Data from Lime Kiln consist of daily determinations of SRKW presence or absence in waters visible from the park viewing area, collected by experienced observers with consistent daily effort from May through August of each year (Olson et al. 2018). A zero in the daily observation data from this location can be interpreted as a true absence of SRKWs at this local scale.

Additional data on presence of SRKWs in the broader Salish Sea region are available in the Orca Master Database (Olson et al. 2018, The Whale Museum 2018). These data include public reports to The Whale Museum and other sightings networks (e.g. OrcaNetwork, 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 come from most areas of the Salish Sea (Fig. 1) and extend as far back as 1948, although dedicated effort to track SRKW presence in the region began in 1978 (Figs. S2 & S3, and Olson et al. 2018).

2.3.2. Salmon data

For SRKW prey data, we rely on a Chinook salmon test fishery at Albion, British Columbia (Fig. 1, Table S1), which has tracked the spawning migration of Chinook salmon to the Fraser River system since 1981. The test fishery is a gill net survey with consistent, standardized methodology, allowing for a robust index of the timing and abundance of the migration (Fig. S4, and Parken et al. 2008). Data consist of catch per unit effort (CPUE), collected daily from the start of April to the end of August, and every other day from September through mid-October (data available at https://www.pac.dfo-mpo.gc.ca/fm-gp/fraser/docs/commercial/albionchinook-quinnat-eng.html). These data provide a relevant comparison to the Lime Kiln SRKW observations because many Chinook salmon returning to the Fraser River (across multiple populations with divergent migration timing) pass through the area where Lime Kiln is located (Parken et al. 2008, WDFW 2020). Chinook salmon make up 50–90% of SRKW diet during the spring

and summer months, and ~80–90% of the Chinook salmon consumed by SRKWs in the San Juan Island area from May to September originate in the Fraser River watershed (Hanson et al. 2010, 2021).

For the broader, regional dataset, ideally we would compare SRKW timing in the Orca Master database to salmon timing in the same waters. However, to our knowledge, spatially explicit daily or weekly data of salmon abundance across the full extent of these regions are not available. We therefore used data from watersheds where adult salmon arrive after passing through the 2 core regions in Fig. 1. For the central Salish Sea region, we used the Albion Chinook salmon test fishery data described above (see previous paragraph), but extended to the full monitoring period (i.e. through mid-October). For Puget Sound proper, we used stream count data for adult coho, chum, and Chinook salmon, available from the Washington Department of Fish and Wildlife (https://wdfw.wa.gov/fishing/management/hatcheries/escapement). Daily or weekly data are available for 67 Puget Sound tributary streams since 1997 and include wild and hatchery counts. We narrowed this to 13 index runs based on criteria of proximity of the count site to Puget Sound (<25 km), time series duration (≥5 yr, with frequent monitoring in each year), and relatively large run size (mean counts from trap estimates of 1400–30000 for chum, 621–11500 for coho, and 550–13350 for Chinook). The 13 index runs included at least 3 runs from each of the 3 salmon species, comprising hatchery and/or wild populations in 7 streams (Table S2). We include all 3 salmon species because the breadth of SRKW diet increases and can include chum and coho salmon during the fall and winter months when SRKWs use Puget Sound proper (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.

Additional details of the datasets can be found in Text S1 in the Supplement.

2.4. Analyses

2.4.1. Modeling phenology of SRKWs

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 modeling (similar to Moussus et al. 2010, Strebel et al. 2014), 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 peak occurrence, as well as total annual estimated whale days for Lime Kiln (quantified by summing daily occurrence probabilities across all days in a year). First and last likely occurrence were not quantified for this dataset because of the censored nature of data collection (i.e. from May through mid-August).

Unlike the Lime Kiln dataset, the regional-scale Orca Master data are not collected with consistent effort or standardized methodology. Rather, they are often opportunistically collected, and thus likely to be biased in space (e.g. whale locations are unknown if they are not observed in the Salish Sea). Observation effort is also not standardized over time for these data. For example, with increasing public awareness of SRKWs, there has been a dramatic increase in reported sightings since 1978, especially following the establishment of internet-based reporting in 2000 and subsequent rises in social media (Olson et al. 2018). Furthermore, Orca Master data do not include absence observations (i.e. true observations of zero whales present), which are essential for quantifying phenophases such as first and last days of occurrence. This adds to model uncertainty and forces additional modeling steps such as estimating 'pseudo-absences.' See Text S1 for more information.

We used Orca Master sightings data to approximate SRKW presence in 2 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 are most aligned with mean SRKW seasonal patterns over time (Olson et al. 2018). We analyzed the Orca Master sightings data to derive estimates of daily occurrence probabilities, summed annual modeled occurrence probabilities for annual estimates of 'whale days' (days with whales present), and first, last, and peak-occurrence dates from 1978 through 2017 in the central Salish Sea and Puget Sound proper (Figs. 1 & S1).

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 1 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 to the state model (Kéry & Royle 2016). We modeled this as a binomially distributed variable, the number of sightings of the pod per day at each site ('sites' in our model are Washington state marine areas, https://wdfw.wa.gov/fishing/locations/marine-areas) out of the total number of sightings in the site that day (similar to Strebel et al. 2014). We fit separate hierarchical occupancy models for each pod, region (central Salish Sea and Puget Sound proper), and season (spring/summer vs. fall/winter), accounting for non-independence of year with random effects, to estimate daily occupancy probabilities. We then extracted estimates of annual first, last, and peak occupancy dates, and summed daily estimates to generate modeled annual total whale days from each model (see Text S2 for details). Modeled estimates were similar to raw values of observed whale days (see Text S3 for details).

2.4.2. Modeling phenology of salmon

To characterize the phenology of Fraser River Chinook salmon, we fit a hierarchical thin-plate regression spline model to the Albion test fishery dataset, in which the response variable (logged CPUE) was continuous and normally distributed. As with the SRKW model, we modeled day of year with a smooth function, and year as a level. We used this model to estimate first occurrence day (defined as the first day of the year with CPUE > 0.005) and peak occurrence day (peak CPUE day of year) for comparison with the Lime Kiln dataset. Last occurrence day, or the last day of the year with CPUE > 0.005, was quantified in comparisons across the full central Salish Sea region (see next paragraph). We also summed all daily CPUEs from April to 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. S2; see also Parken et al. 2008, Chamberlain & Parken 2012).

To characterize the phenology of salmon migrations in the central Salish Sea, we used the hierarchical thin-plate regression spline model fit to Albion test fishery data (as described in the previous paragraph), with the small difference that the full seasonal period of the dataset was utilized (i.e. through October). Thus, in this comparison, we used the model to estimate first (defined as the first day of the year with CPUE > 0.005) and last occurrence (the last day of the year with CPUE > 0.005), as well as peak CPUE day of year. For Puget Sound proper, we fit separate models to each of the 13 Puget Sound index 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. We treated distinct rivers and species, as well as hatchery vs. wild types of the same species, as separate groups in our model.

We assessed model performance through commonly used Markov Chain convergence and efficiency diagnostics, including R_{hat}, which compares the between- and within-chain estimates for model parameters (all were close to 1) and effective sample size (n_{eff}, which were high), as well as visual consideration of chain convergence and posteriors (Gelman et al. 2021). For additional analytical details and code, including model equations, see Texts S2–S4, Codes S1–S3 in the Supplement. Given recent criticism of conventional 95th percentile uncertainty intervals (e.g. McShane et al. 2019), we follow the suggestion of McElreath (2018) to include a series of nested intervals: 50th, 75th, and 95th percentile uncertainty intervals are presented in Tables S3 & S4. Throughout the main manuscript, we present 75th percentile uncertainty intervals in the graphs (see Figs. 3–5) and text.

3. RESULTS

We find that timing of SRKW occurrence has shifted in their summer core habitat within the central Salish Sea, with the day of year of peak occurrence probability shifting later at rates of 1–5 d yr^{-1}. The shifts, which vary by pod, time period (e.g. 1978–2017 vs. 2001–2017), and location (i.e. Lime Kiln vs. the whole Salish Sea region), are consistent with shifts in Fraser River Chinook salmon (peak abundance and first likely occurrence dates delayed at rates of 2.3 and 0.8 d yr^{-1}, respectively). The shift in timing of fall/winter SRKW occurrence in the Puget Sound, however, is not consistent with shifts in salmon populations returning to nearby rivers.

3.1. SRKW phenology

Over the past quarter century (1994–2017), phenology and presence of SRKWs shifted considerably at Lime Kiln (Figs. 3A, S5 & S6): across all pods together, the day of year corresponding to peak probability of occurrence has become later at a rate

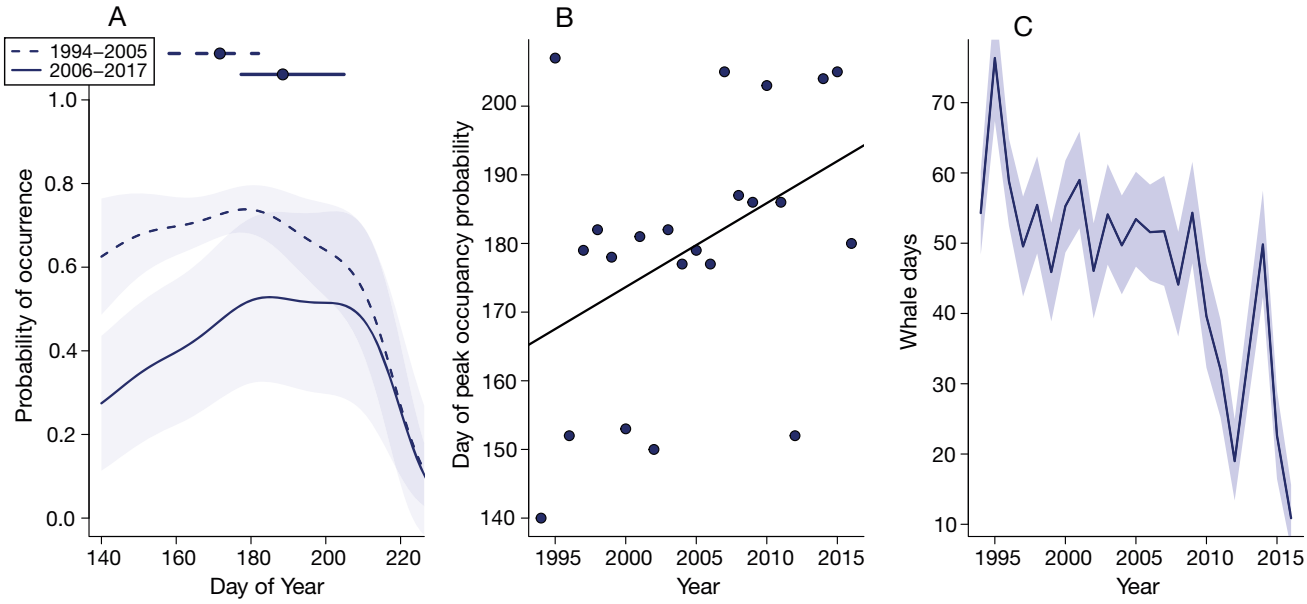

Fig. 3. Southern resident killer whale (SRKW) phenology and presence has shifted at Lime Kiln Point State Park, a site with consistent observations from May (day of year 140) through August (day of year 225) in the central Salish Sea. (A) Timing of SRKWs has delayed in recent (solid line) vs. earlier (dashed line) years, with day of year of peak occupancy probability shifting from a mean of 168 in 1994–2005 to 192 in 2005–2017 (points at top of panel, with error bars). (B) Across the full time series, the day of peak occupancy probability has delayed at a rate of 12.2 d decade^{-1} (slope of regression line shown). (C) SRKW pods are spending fewer days at Lime Kiln in recent decades; this is also associated with lower probability of occurrence in recent years (A). Shading and error bars: 75% uncertainty intervals. Patterns here are for all SRKW pods together; see Fig. S6 for each pod separately. Changing the breakpoint to 2007 or 2005 did not qualitatively alter results (Fig. S7)

of 1.2 d yr^{-1} (75% CI: 0.52–1.90). This corresponds to a shift of 29.3 d (75% CI: 12.5–46.2) across the 24 yr 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 d 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 3 pods (Fig. S6). Using a breakpoint of 2005 or 2007 did not qualitatively alter results (Fig. S7). First likely occurrence dates (for all pods together) were delayed at a rate of 0.3 d yr^{-1} (75% CI: 0.1–0.6), and last occurrence dates did not change consistently in this dataset.

As with the systematic observations at Lime Kiln, our analysis of the Orca Master sightings database for the central Salish Sea region as a whole suggests there has been tremendous variability in the estimated peak occurrence probability for SRKWs (ranging over a 4 mo period from May 1 to September 1 in any specific year, Fig. S8). However, despite this variability, it is clear that since 2001, peak occurrence probability for SRKWs has shifted later in the year in the central Salish Sea region as a whole for J pod (Fig. S8) and, to a lesser degree, K pod (Fig. S9). Although the predicted probability of occurrence for J pod in the central Salish Sea region in spring (April through June) was near 1.0 from 2001 to 2008, since 2009 the expectation is much lower (<0.5 probability of occurrence in April) and does not approach 1.0 until nearly July (Fig. S8). In addition, the overall mean occurrence probability across the season has declined >25% for J pod from 2001 through 2017 (from 0.86 to 0.64). 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. 1.01 d yr^{-1} delay from 1978–2017 vs. 6.49 d yr^{-1} delay from 2001–2017 for J pod; Table S4). J pod exhibits the most pronounced delays of the 3 pods; patterns for K and L pods vary (Figs. 4A, S8–S10).

As in the central Salish Sea, in Puget Sound proper, the day of first SRKW occurrence has delayed since 2001 for all 3 pods (Fig. 4B). Trends in peak and last occurrence dates vary across pods. For example, peak and last occurrence dates are delaying for K pod, but peak occurrence probability date has not shifted consistently for J and L pods (Fig. 4B). The day of peak occurrence is variable, but ranges over a 2 mo period (from late September to early December)

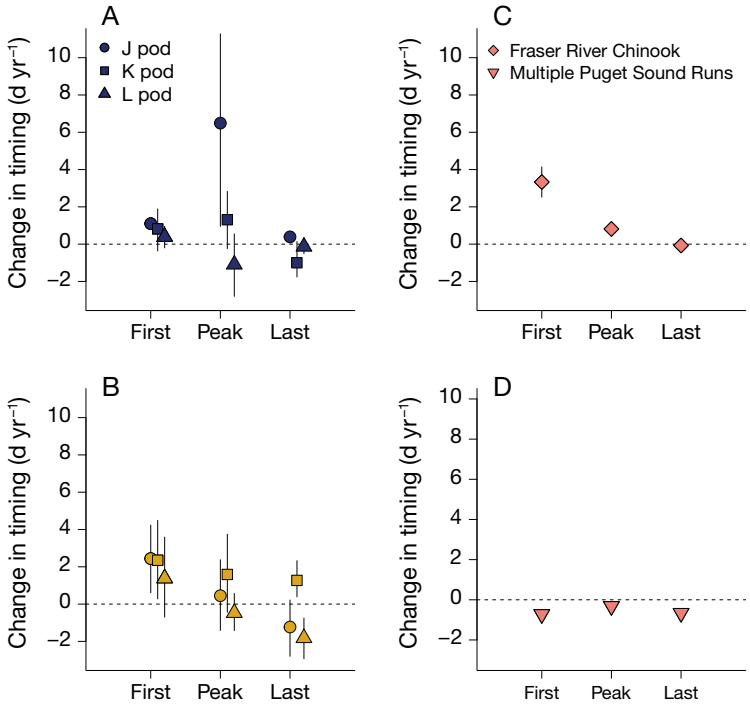

Fig. 4. Trends in (A,B) southern resident killer whale (SRKW) and (C,D) salmon phenology in (A,C) central Salish Sea and (B,D) Puget Sound proper from 2001 through 2017. SRKW shifts are summarized from linear models fit to estimates of day of year of first day of likely occurrence (probability of occurrence >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 (from April through October) and from a hierarchical linear model fit to escapement data across 13 distinct groups (including 3 species of wild and hatchery origin across 7 different streams) for Puget Sound proper. Error bars: 75% uncertainty intervals (95% uncertainty intervals are in Table S4)

rather than a 4 mo period (Figs. S8–S10, panels C & D). Mean occurrence probability has declined in Puget Sound proper since 2001, for J (Fig. S8C) and L pods (Fig. S10C), but uncertainty intervals are wide for the period 2001–2008. Across the full dataset (1978–2017), the trend has been toward later peak occurrence for all 3 pods (delaying at rates of 1.17 (75% CI: 0.71–1.61), 1.75 (75% CI: 1.21–2.27), and 1.07 (75% CI: 0.71–1.43) d yr^{-1} for J, K, and L pods, respectively (Table S4).

3.2. Salmon phenology

Over the same time period, the phenology of returning adult Fraser River Chinook salmon caught in the Albion test fishery shifted in the same direction as SRKW phenology (Fig. 5, Table S3): peak abundance dates delayed at a rate of 2.3 d yr^{-1} (75% CI: 1.7–3.0), and spring first likely occurrence dates delayed at a rate of 0.8 d yr^{-1} (75% CI: 0.2–3.1). This corresponds to delays of 55.2 d (75% CI: 40.8–72.0) for peak abundance index date (Fig. 5B) and 19.2 d (75% CI: 4.8–74.4) for first likely occurrence date across the 24 yr dataset. Comparing the 1994–2005 and 2006–2017 periods, peak mean daily estimated CPUE for salmon shifted ~40 d later on average (Figs. 5A & S7). 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. 5C). Adult salmon returns in Puget Sound, on the other hand, shifted toward slightly earlier returns (advancing rates of −0.4 to −0.7 d yr^{-1}, on average across all 13 runs; Fig. 4D).

3.3. Coupled phenological shifts in SRKWs and salmon

Taken together, these results suggest that predator (SRKW) timing may be related to prey (Chinook salmon) timing and abundance at Lime Kiln. Later dates of peak abundance of Fraser River Chinook salmon are associated with later peak SRKW occurrence probability at Lime Kiln (slope = 1.43, $r^2 = 0.31$, p = 0.006; Fig. 6). Furthermore, the number of whale days has declined at Lime Kiln from 1994 to 2017 (Fig. 3), tracking declines in the Chinook salmon abundance index (from the Albion test fishery annual summed CPUE, Fig. 5). Whale days declined at a rate of −1.7 d yr^{-1} (75% CI: −2.0 to −1.3), resulting in 85% fewer observations in 2017 than in 1994 at Lime Kiln (Fig. 3; see Fig. S6 for separate pods). Since 2001, the decline is even steeper (−2.4 d yr^{-1}, 75% CI: −3.0 to −1.7). However, in contrast to Lime Kiln, trends in SRKW occurrence are opposite of those quantified for adult salmon returns in Puget Sound proper.

4. DISCUSSION

Developing management strategies that incorporate phenology of interacting species is critical, especially for threatened and endangered species. Failure to apply the right management measure at the right time — such as minimizing human activity during sen-

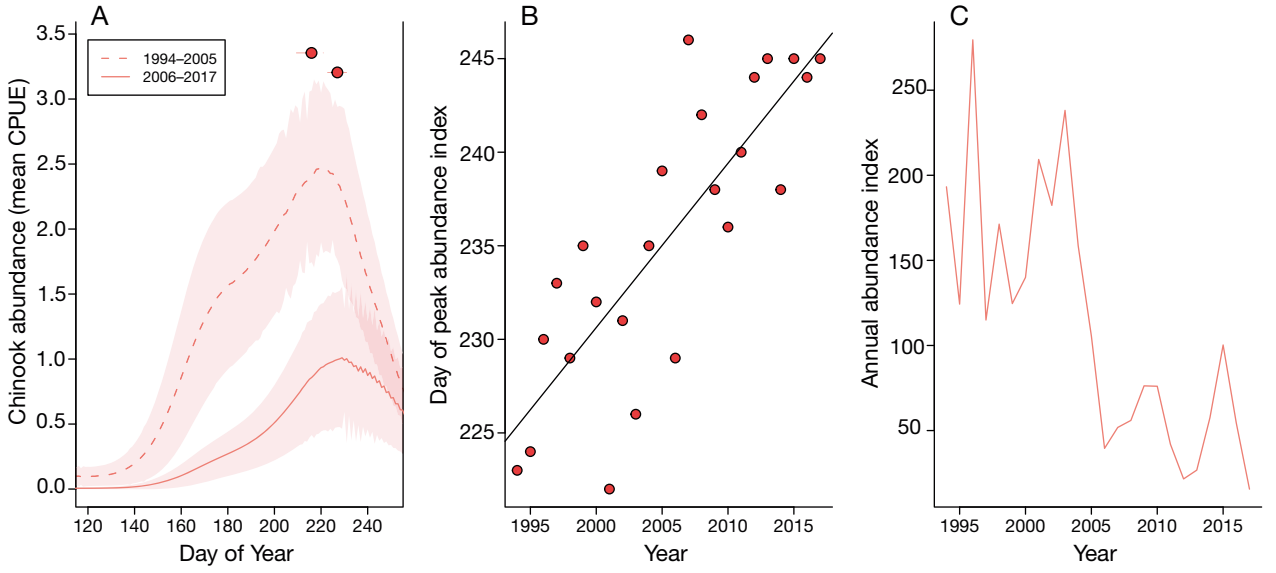

Fig. 5. Timing and abundance index has shifted in Fraser River Chinook salmon, a favored prey of southern resident killer whales as they travel past the area around Lime Kiln Point State Park during spawning migration (data from Albion test fishery, which encompasses multiple distinct runs). (A) Timing of peaks in the abundance index has delayed in recent (solid line) compared with earlier (dashed line) years, due largely to a reduction in the spring run; the day of year of peak abundance index has shifted from a mean of 198 in 1994–2005 to 233 in 2005–2017 (points at top of panel, with error bars). Shading and error bars: 75% uncertainty intervals. (B) Across the full time series, the day of peak abundance index has delayed at a rate of 27.5 d decade^{-1}. (C) Total abundance index across the spring through fall seasons has also declined in recent decades. Changing the breakpoint in (A) to 2007 or 2005 did not qualitatively alter results (Fig. S7). CPUE: catch per unit effort; shading and error bars: 75% uncertainty intervals

sitive breeding periods (Pearson 2003) — can lead to undesirable social and biological outcomes. Similarly, application of a management measure focused at the wrong time can lead to unintended conservation challenges. For example, delayed opening of the California Dungeness crab *Metacarcinus magister* fishery in 2016, in combination with changing ecosystem conditions that caused large whales to feed within crab fishing grounds over an unusually long period of time, led to an unanticipated and substantial increase in whale bycatch (Santora et al. 2020, Samhouri et al. 2021). Though recent shifts in the timing of biological events have been quantified in diverse species and ecosystems around the world (Poloczanska et al. 2013), the potential for match–mismatch dynamics and the implications of phenological shifts remain poorly understood (Paton & Crouch 2002, Morellato et al. 2016, Kharouba et al. 2018). Here we use extensive datasets to show that the timing of SRKW presence in the Salish Sea has shifted over the past 40 yr. This suggests that management strategies 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 a key prey resource, Chinook salmon (Figs. 3–6).

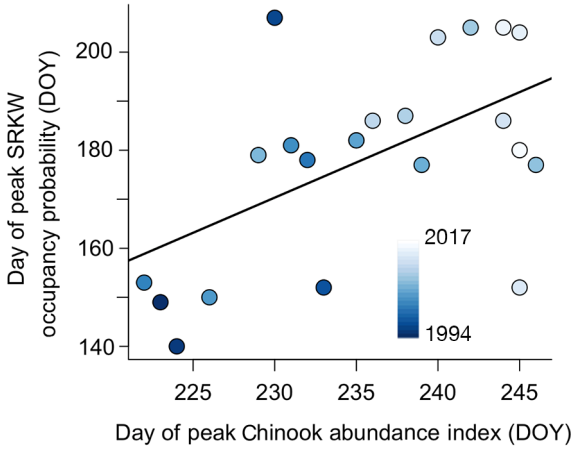

Fig. 6. Southern resident killer whale (SRKW) phenology has shifted, in concert with shifts in Fraser River Chinook salmon. Dates of peak probability of occurrence for SRKWs (all pods together) at Lime Kiln Point State Park (in the central Salish Sea) are positively associated with dates of peak abundance index for Fraser River Chinook salmon (slope = 1.43, r^2 = 0.31, p = 0.006). DOY: day of the year

Our findings 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 (Armstrong et al. 2016, Aikens et al. 2017, Abrahms et al. 2021). 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 correlated 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 first and peak occurrence by SRKWs (J and K pods, specifically) corresponds to later arrival of Fraser River Chinook salmon (Fig. 4). While additional work is needed to disentangle the many potential factors influencing shifts in the timing of SRKW occurrence 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 correspondence may not be surprising, given the numerous other observations of consumer phenological tracking and even altering the spatiotemporal patterns of resource waves (Armstrong et al. 2016, Abrahms et al. 2019, Geremia et al. 2019). At first glance, this might appear to allay concerns over phenological mismatch with climate change (Kharouba et al. 2018), but this work highlights that though phenological tracking may be a beneficial response to climate change (Abrahms et al. 2021), it is not always sufficient. The delay in the peak abundance timing of Fraser River Chinook salmon is driven primarily by a collapse of spring Fraser River Chinook populations (Fig. 5; see also Riddell et al. 2013), 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 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). The potential for this 'phenological cascade' is all the more likely for SRKWs, as they are specialists with relatively narrow resource requirements, which presents demographic challenges when prey, habitat, and other factors change (Abrahms et al. 2021).

Our findings in Puget Sound proper were more equivocal than those in the central Salish Sea, suggesting either insufficient data to estimate shifts or that resource timing may not be the sole driver of consumer phenology. Based on our model estimates in Puget Sound proper, SRKW presence does not appear to be shifting coincidently with shifts in salmon migration timing (Fig. 4). However, this result may be at least partially due to the fewer observations in the region compared with the central Salish Sea region (Figs. S2 & S3), especially earlier in the time series, prior to social media and other rapid communication tools. The opportunistic, crowd-sourced database on which we relied is not equivalent to systematically collected data that emerge from cooperative, scientific monitoring programs (Kosmala et al. 2016, Ghermandi & Sinclair 2019); it is impossible to fully disentangle true absence of SRKWs from simply an absence of reported observations by humans, even with our use of novel statistical tools that incorporate effort (see Text S4, Fig. S11). Additional systematic efforts would bolster the information available to inform conservation and management decisions that directly and immediately (e.g. salmon harvest), or indirectly and with time lags (e.g. salmon hatchery practices), influence SRKW movement and behavior.

If we assume, however, that our models are a reasonably accurate representation, the divergent trends in SRKW phenology from their prey in Puget Sound proper may indicate that SRKWs are tracking an alternative prey source (e.g. other populations of Chinook salmon, or other prey species), or that SRKW movements are tuned to other factors. Contemporary phenology of this highly mobile species may be driven more strongly by other environmental cues (e.g. temperature or precipitation, Chmura et al. 2019), social cues, learning, and memory (Brent et al. 2015, Samplonius & Both 2017, Jesmer et al. 2018, Abrahms et al. 2019). Human activity, and vessel traffic and noise in particular, can affect movement and behavior of SRKWs and other marine animals (e.g. Lusseau et al. 2009, Noren et al. 2009), and may be an increasingly strong environmental influence on this endangered population.

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 (Furey et al. 2011, Armstrong et al. 2016, Morellato et al. 2016). 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 the US Endangered Species Act Section 7) as well as broader efforts such as ecosystem-based 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). For example, in the case of SRKWs, knowledge of the timing of their movements to inland waters in relation to salmon abundance and migration timing could be used to modify in-season salmon fisheries harvest practices.

Our work underscores challenges associated with conservation of endangered predators such as SRKWs. Although reduced prey availability is a clear threat facing this endangered population, ameliorating the threat by increasing salmon abundance is not straightforward. Quantifying predator and prey co-occurrence in space and time, as we have done here for salmon and SRKWs, provides necessary, though not sufficient, background information for developing focused and effective management efforts to enhance prey availability, through actions such as hatchery production, restrictions on salmon harvest, removal of dams on salmon rivers, salmon habitat restoration, and predator culling (Berdahl et al. 2017, SROTF 2019). Critical gaps remain in our mechanistic understanding of links between these potential management actions, their timing, and consequences for SRKWs. For example, 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. 2021), but the impacts of changing Chinook hatchery production on the total temporal distribution of prey for SRKWs have not been rigorously investigated.

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. In addition to summarizing trends in habitat use, quantifying spatial and temporal variability across years may help prioritize salmon populations for enhancement. Developing such capabilities will require increasing the robustness of observations and modeling to discern spatiotemporal trends in occurrence, e.g. by identifying ways to include real zeroes in opportunistic datasets where possible. Additional targeted, systematic, standardized observation efforts (akin to Lime Kiln) in other regions of the Salish Sea (e.g. areas where salmon become concentrated and SRKWs are known to feed, such as Admiralty Inlet, Olson et al. 2018) or expanding permanent hydrophone networks (e.g. https://www.orcasound.net/) would make current data more readily available for SRKW recovery efforts. Additional information on prey stocks in different regions and seasons will also be critical to fully understand shifts in phenology of the portfolio of salmon and other prey consumed by SRKWs (Hanson et al. 2021, Sullaway et al. 2021).

SRKW recovery and salmon enhancement are large, complex, and expensive problems (cost estimates are >$1 billion, SROTF 2019), and tackling them requires synthesis of all available information. In this paper, we have analyzed the largest available database on SRKW presence, and quantified shifting temporal patterns in their presence at local and regional levels. Across fine to broad scales, integrating phenology and phenological shifts explicitly is likely to enhance effectiveness of conservation efforts under global change.

Data and code availability. The subset of Orca Master data and other data used in these analyses, as well as all code, are available at https://github.com/AileneKane/srkwphen. The full Orca Master Database can be requested by contacting The Whale Museum, https://whalemuseum.org/. Albion test fishery data are available at https://www.pac.dfo-mpo.gc.ca/fm-gp/fraser/docs/commercial/albionchinook-quinnat-eng.html. The WDFW escapement data are available at https://wdfw.wa.gov/fishing/management/hatcheries/escapement.

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