ARTICLE

Marine Mammal Science 🐋

Traditional summer habitat use by Southern Resident killer whales in the Salish Sea is linked to Fraser River Chinook salmon returns

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Abstract

Southern Resident killer whales (SRKW, *Orcinus orca*) are a small, endangered population of fish-eating killer whales that inhabit coastal and inland waters of the western United States and British Columbia. SRKW have been in decline since 1995, with food availability, vessel disturbance, and pollutants proposed as drivers of their decline. We used 17 years of sightings data from the SRKW core summer habitat in the Salish Sea to examine trends in presence of SRKW, and how these trends may be related to the availability of a key food source, Fraser River-origin Chinook salmon. We found that SRKW occupancy has declined by more than 75%, in step with reduced average catch per unit effort (CPUE) of Fraser River Chinook salmon. J pod was present in the core summer habitat most often, followed by K and L pods. All three pods demonstrated declines in visitation to the core summer habitat from 2004 to 2020, and presence of SRKW was significantly related to annual average Fraser Chinook CPUE. Our findings suggest that declining Fraser River Chinook returns may be reaching a point where SRKW cannot reliably meet their energetic needs, driving them to forage in areas outside of their traditional core summer habitat.

1 | INTRODUCTION

Southern Resident killer whales (SRKW, *Orcinus orca*) are a small population of fish-eating killer whales that inhabit coastal and inland waters of the western United States and British Columbia (Ford et al., 1998). The SRKW population is comprised of three matrilineal pods, referred to as J, K, and L pods. K and L pods range widely, particularly in winter and spring, with observations as far north as southeast Alaska and as far south as central California. J pod, in contrast, is more commonly encountered in the Salish Sea, and all three pods are routinely encountered in the Salish Sea during summer months (Hanson et al., 2017; National Marine Fisheries Service, 2019). The SRKW population has been in decline since 1995 and is listed as endangered under both the U.S. Endangered Species Act and the Canadian Species at Risk Act (Fisheries and Oceans Canada, 2008; National Marine Fisheries Service, 2019). Three main stressors have been proposed as possible drivers of the SRKW population decline: (1) high levels of persistent organic pollutants and other toxicants in their core habitat range (and in their tissues) that could impact survivorship and fecundity (Krahn et al., 2009); (2) disturbance by vessels in the heavily-trafficked Salish Sea, which could impact their foraging efficiency (Holt et al., 2021; Lusseau et al., 2009); and (3) declining availability and energetic content of their primary prey, Chinook salmon (*Oncorhynchus tshawytscha*), which may be leading directly to poor condition of SRKW and decreased survival probability (Ford et al., 2010; Ohlberger et al., 2018; Stewart et al., 2021).

SRKW feed exclusively on fishes, with Chinook salmon making up the majority of their diet, and smaller contributions from other salmon species, flatfish, and groundfish (Ford et al., 2016; Hanson et al., 2010). The summer and fall diets of SRKW, in particular, appear to be composed largely of Chinook salmon returning to tributaries in the Salish Sea, including the Fraser River and Puget Sound (Hanson et al., 2021). Similarly, analyses of body condition (Stewart et al., 2021), demographic rates (Vélez-Espino et al., 2014), and the timing of SRKW visitation to the Salish Sea (Ettinger et al., 2022) all suggest that SRKW health, population dynamics, and movement patterns may be influenced by Fraser River and Puget Sound Chinook returns. Traditionally, all three matrilineal family units have been found regularly in the central Salish Sea between April and October (Olson et al., 2018), in what has been designated as their core summer habitat (National Marine Fisheries Service, 2008; Figure 1). Accessing high densities of returning Chinook salmon in the Salish Sea during this summer foraging period appears to be important for building up blubber stores prior to the winter and early spring period when prey may be lower quality and more dispersed along the outer coast of the U.S. and Canada (Hanson et al., 2021). This potential importance is reflected in the interannual seasonal decline in SRKW body condition (Fearnbach et al., 2020).

Understanding how SRKW foraging behavior is influenced by prey availability in their traditional core summer habitat is important in developing strategies to support the recovery of this endangered species. The abundance of returning Fraser River Chinook may be a key driver of SRKW foraging behavior and habitat use from April through September, as Fraser River Chinook generally have larger individual body sizes (and therefore higher energetic value as prey) than other Salish Sea Chinook stocks (O'Neill et al., 2014), and make up an estimated 40%–50% of Chinook salmon that are present in the Salish Sea during the summer months (Stewart et al., 2021). Here, we explore how traditional core summer habitat use by SRKW is related to the abundance of returning Fraser River Chinook salmon. We use nearly two decades of compiled observations of the daily presence of each pod, and a higher resolution 7-year data set on the daily abundance of SRKW to evaluate seasonal trends in SRKW use of core summer habitat, and pod-level relationships to Fraser River Chinook returns.
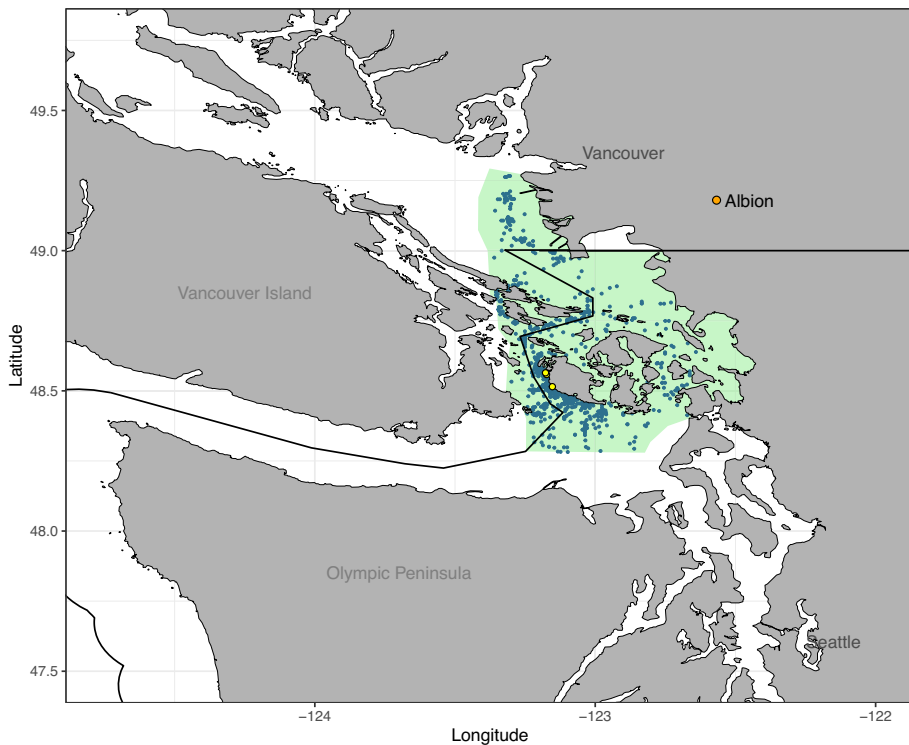
FIGURE 1 Traditional core summer habitat for Southern Resident killer whales. Green shading indicates the traditional core summer habitat area, spanning both United States and Canadian waters. Blue points indicate sighting locations of SRKW 2014–2020. The black line indicates the United States Exclusive Economic Zone and the border between the U.S. and Canada. The orange point indicates the location of the Albion test fishery, in Albion, British Columbia on the Fraser River. The yellow points indicate locations of hydrophones used to detect SRKW and supplement sightings reports.

2 | METHODS

2.1 | Sighting data collection

Sightings data were compiled from April 1 to October 31 for each year, from different sources throughout the core summer habitat range. From 2004 to 2013, sightings data were collected with resolution to the pod level, whereas from 2014 to 2020 sightings data were resolved to the individual whale level. Data sources included:

(1) Center for Whale Research encounter data (individual level 2004–2020): photographs collected during field research activities as well as photos contributed by members of the public and verified by CWR researchers (Center for Whale Research, 2020).

(2) Photo-identification data (individual level 2008–2020) collected by authors JWD and HF during aerial photogrammetry field efforts (Fearnbach et al., 2020; Stewart et al., 2021).

(3) First-hand reports from the public provided to Orca Network (https://www.orcanetwork.org) with accompanying photographic and video confirmation (pod and individual level 2004–2020).

(4) First-hand reports from naturalists, field researchers, and individual sighting data contributors provided directly to J.C. with accompanying photographic confirmation (pod level 2004–2020; individual level 2014–2020).

(5) Hydrophone detections from the west side of San Juan Island (2014–2020). Although sightings data were based primarily on visual reports, live hydrophone streams and hydrophone recordings from Lime Kiln State Park

(https://www.smruconsulting.com/lime-kiln-live-hydrophone), Haro Strait (https://www.orcasound.net), and a privately owned hydrophone on San Juan Island were used to supplement visual sightings data and fill detection gaps. For example, hydrophone recordings were frequently used to pinpoint the time at which a pod arrived or departed from the region after visual sightings were reported from another source listed above. Detections were identified to the pod level using pod-specific call types (Ford, 1987).

(6) For 2004–2011 and 2014, supplemental sightings reports (pod level) were extracted from the 2012 NOAA/Whale Museum Orca Master database (Olson et al., 2018).

Sightings from all of the above sources were summarized into a single daily record for each pod; either presence/absence for 2004–2020, or number of whales for 2014–2020. For the count data from 2014 to 2020, if the same pod or whales were sighted by multiple sources in a given day, the total number of individual whales confirmed by photo identification across all sources was considered the count for that day.

Quantifying effort from six disparate sightings sources is extremely challenging. To develop metrics of relative survey effort, we compiled sightings of a suite of cetaceans that were recorded by JC from sightings reports (and hydrophone detections of killer whales), using the same sighting sources as SRKW. We recorded the number of days with reports of gray (*Eschrichtius robustus*), humpback (*Megaptera novaeangliae*), minke (*Balaenoptera acutorostrata*), and transient (Bigg's) killer whales in the SRKW traditional core summer habitat as a proxy for the number of days with survey effort in the region throughout the study period. In addition, we compiled sightings reports from the same sources for SRKW both inside and outside the core summer habitat, to determine the number of days that SRKW were accounted for in total as an indicator of detection probability and whether days with no SRKW sightings in the core habitat reflect true absences. These cetacean sightings data were only available for 2014–2019 from gray, humpback, and minke whales, and 2014–2020 for transient killer whales.

SRKW social structure is complex, with dynamic associations between individuals changing through time to form different numbers of social clusters both at the pod level and the population level (Parsons et al., 2009). In addition, while the population is conventionally split into three matrilineal pods, individuals that are natal members of a pod do not always remain associated with that pod permanently. Although uncommon, a small number of whales in our sightings data set have routinely associated with pods outside their family groupings throughout the study period. For example, whale L87, a natal member of L pod, began associating with K pod in 2006 after his mother died. Starting in 2010, L87 associated with J pod for almost a decade until he returned to L pod in late 2019. Whales L7, L53, and L57 all similarly associated with J pod during some years in the core summer habitat. In order to remain consistent with the pod-level designations used in the majority of previous studies focused on SRKW and examine pod-level differences in presence and abundance of SRKW in the core summer habitat, we excluded records of these four whales from our data set to avoid situations where their presence while associating with J pod would inflate the reported presence or abundance of L pod whales in cases where the rest of L pod was absent. We note that because all of these whales were from L pod, their exclusion could lead to a slight positive bias in the mean number of L pod whales sighted in the core summer habitat (by eliminating cases where only one of the above whales is present), and a slight negative bias in the mean occurrence of L pod for the same reason.

2.2 | Salmon data

We used daily gill net catch per unit effort (CPUE) data on Chinook salmon returning to Fraser River tributaries that are collected by the Albion test fishery at the mouth of the Fraser River (https://www.pac.dfo-mpo.gc.ca/fm-gp/fraser/docs/commercial/albionchinook-quinnat-eng.html). We chose this metric of returning Fraser River Chinook relative abundance as it is most likely to closely represent the availability of Chinook salmon to SRKW in the core summer habitat area, and has finer temporal resolution for evaluating seasonal trends than available estimates of at-sea total Chinook abundance (e.g., Fishery Regulation Assessment Model, FRAM; Pacific Fishery Management Council, 2008). The Albion test fishery does not collect Chinook CPUE data every day of the year. For each year, we
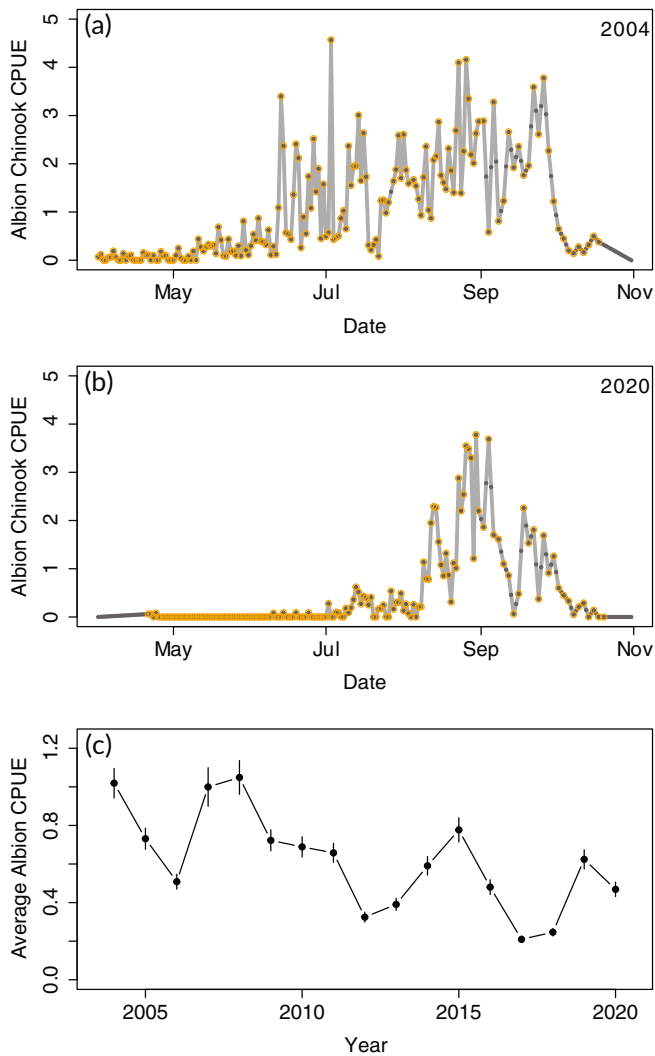
FIGURE 2 Albion test fishery Chinook catch per unit effort. Panels (a) and (b) show daily CPUE in the Albion test fishery in 2004 and 2020, respectively. The dark gray points indicate daily CPUE values used as inputs in the generalized additive model analyses. The orange circles indicate days with recorded CPUE data, whereas points without orange circles indicate interpolated values. Annual mean CPUE values (not including interpolated CPUE) are shown from 2004 to 2020 in (c). Vertical bars in (c) indicate the standard error of mean CPUE values.

set the CPUE values for April 1 and October 31 to zero, unless a sample was collected on that day, as these dates are close to the beginning and end of the expected migration timing of the combined spring, summer and fall Fraser Chinook runs. We then estimated missing values using a simple linear interpolation (Figure 2, Table S1). Finally, we moved the observed and interpolated CPUE values forward by 10 days to account for the approximate time it would take a Chinook salmon to migrate from the central San Juan Islands to the mouth of the Fraser River (Ayres et al., 2012; Ettinger et al., 2022). In addition to daily CPUE values, we calculated the average daily CPUE in the Albion test fishery from April 1 to October 31 for each year from 2003 to 2020, excluding interpolated values. Our final salmon metrics for inclusion in the following analyses were (1) the daily interpolated Albion CPUE, with a 10-day lead; (2) the mean daily CPUE for the contemporary year; and (3) the mean daily CPUE from the previous year.

2.3 | Data analysis

For coarse inference and visualization purposes we used simple linear regressions to examine relationships of year and mean annual CPUE with the number of days each pod was present in the core summer habitat (2004–2020), and the number of whales from each pod on days when that pod was present (i.e., excluding zeros; 2014–2020). We calculated the occupancy proportion as the number of days each pod was observed within the core summer habitat divided by 215 (the number of days between April 1 and October 31).

Next, to account for a variety of potential drivers of SRKW occupancy in the Salish Sea, we used generalized additive models (GAMs) to examine relationships between SRKW attendance and pod membership, day of the year, daily Chinook salmon CPUE, and annual mean CPUE (contemporary and lagged). We chose to use GAMs as we hypothesized that some relationships with SRKW attendance (e.g., day of year) may exhibit nonlinear responses. We conducted two separate GAM analyses for the two different levels of resolution in the sightings data. First, we conducted an analysis of the full 2004–2020 data set at the pod resolution level, using a binomial response model for presence/absence of each pod. The input data were structured such that the response variable was presence (1) or absence (0) within the traditional core summer habitat area (Figure 1), and each record was associated with a pod (J, K, or L), and the corresponding covariates for that observation (day of the year, daily Chinook CPUE, and annual mean CPUE). We included fixed effects for pod and year, and smooth terms for day of the year, mean contemporary CPUE, mean lagged CPUE, and contemporary daily CPUE. For all smooth terms, we estimated an independent smooth for each pod. We fit the model using the R package *mgcv*, where the model was defined as:

$$\text{Presence} \sim s(\text{Day of Year}, by = \text{Pod}) + s(\text{Mean CPUE}, by = \text{Pod}) + s(\text{Lagged Mean CPUE}, by = \text{Pod}) + s(\text{Daily CPUE}, by = \text{Pod}) + \text{Pod} + \text{Year}$$

where s() indicates a smoothed spline fit, Day of Year and CPUE covariates were fit independently for each pod (by = Pod), and the final two terms are the fixed effects of Pod and Year.

Next, we analyzed the higher resolution individual-level data set from 2014 to 2020. The explanatory variables included in the high-resolution analysis were identical to the terms described above for the binomial model. However, these sightings data included the number of individual members of each pod recorded in the core summer habitat on a given day, making them effectively count data. As such, we evaluated three possible formulations of the above model using (1) a standard Poisson distribution; (2) a zero-inflated Poisson distribution, and (3) a negative binomial distribution. The zero-inflated Poisson distribution estimates the frequency of zeros accounted for by included covariates, as well as "excess" zeros (the zero-inflation component), whereas the negative binomial distribution accounts for overdispersion in the response data including the possibility of many zero counts. These two distribution families potentially better account for overdispersed sightings data that could result from variable survey effort and reporting from the many data sources included in this study. We compared these three model formulations using Akaike's information criterion (AIC; Burnham & Anderson, 2004), and for all models (binomial and count) we examined diagnostic plots of residual distribution and quantiles (Q-Q plots). We evaluated concurvity (the nonlinear analog of multicollinearity) in the estimated effects of covariates in the GAMs using the concurvity() function in *mgcv* and evaluating the pairwise concurvity estimates. Concurvity values are bounded by 0 and 1, where 0 indicates no concurvity and 1 indicates a lack of identifiability between predictor variables. There are no established criteria for identifying unacceptable levels of concurvity, however, we followed (Carvalho et al., 2021; Johnston et al., 2019) in removing one covariate if the pairwise concurvity between two covariates exceeded 0.3. For the final models (binomial and count), we evaluated fit by rerunning the models five times using a different randomly selected subset of 80% of the data each time, predicting the remaining 20% of the data using the fitted model, and comparing the model predictions to the observed values using Pearson's correlation tests and two-sided Wilcoxon rank sum tests. For all models, we used the restricted maximum likelihood to estimate model coefficients. This smoothing method estimates the adjustment and smoothing parameters on the covariate relationships

depending on the type and number of basis functions used to create the smoothing term. Each basis function is multiplied by an overfit penalty value and then summed, resulting in the smoothing function for each parameter. This method penalizes for overfitting in each smoothing function and is recommended when modeling ecological data with GAMs to prevent overfitting (Pedersen et al., 2019).

3 | RESULTS

3.1 | Sighting trends

The number of days that each pod was observed in the core summer habitat between April 1 and October 31 declined steadily between 2004 and 2020 for all pods ($p < .001$; Figure 3). J pod was generally present on more days than K and L pods. The highest years of presence were 2005 for J pod (164 days), 2009 for K pod (124 days), and 2004 for L pod (103 days). The lowest years of presence were 2016 for J pod (36 days), 2017 for K pod (10 days), and 2019 for L pod (10 days). On days when whales were present, there was not a clear pattern in the mean number of whales observed over time ($p > .05$; Figure 3). The mean number of whales present per day ranged from 20.4 to 24.1 each year for J pod, 8.2 to 16.5 for K pod, and 14.9 to 21.4 for L pod. Similarly, whales from all pods were present on more days in years with higher average CPUE in the Albion test fishery ($p < .001$), but there was not a clear relationship between the number of whales present and average annual CPUE ($p > .05$; Figure 3).

From 2014 to 2019, the number of days with sightings of non-SRKW cetaceans—our proxy for relative survey effort—exceeded 85% of the April–October study period, and in 2019 approached 100% coverage (Table 1). Over the same period, SRKW were accounted for both inside and outside the core summer habitat for 37%–76% of the survey period, with 52%–90% of those sighting days inside the core habitat (Table 1). Spatial coverage of sighting reports spanned the Salish Sea from Puget Sound to the Strait of Georgia and the Strait of Juan de Fuca, with few additional sightings on the outer coast of Washington and British Columbia (Figure S1).

3.2 | Generalized additive models

Pairwise concurvity values for all covariates included in the GAM analyses of presence/absence and count data were <0.3, with the exception of contemporary mean Albion CPUE and lagged mean Albion CPUE (pairwise concurvity 0.446 in binomial model and 1 in count models). We therefore removed the lagged mean CPUE from the analyses and reran the GAMs retaining all other covariates.

The GAM analysis of presence/absence data from 2004 to 2020 found significant effects of pod, year, day of year, and mean annual Albion CPUE on the probability of whales being present in the core summer habitat ($p < .01$ in all cases; Figures 4 and 5). The binomial GAM explained 32.3% of the deviance in the data. J pod was most likely to be present between roughly June 1 and October 1, with two peaks in presence around mid-July and mid-September. K pod probability of presence increased steadily until mid-July and plateaued before declining in mid-September. L pod presence peaked in mid-June and plateaued before declining starting in late September. J pod had the highest probability of presence, followed by K pod, and then L pod. The partial effect of year (taking into account all of the other included covariates) fluctuated between 2004 and 2018, with notably negative partial effects in 2019 and 2020. The model estimated a significant smooth term ($p < .001$) for J pod's relationship to daily Albion CPUE (with a 10-day lead). There was an increasing probability of presence with increasing daily CPUE from roughly 0 to 1 CPUE, after which the relationship plateaus and becomes increasingly uncertain (Figure 5). We found no significant relationship between daily CPUE and the probability of whales being present for either K or L pods.

Of the three candidate count models, the standard Poisson GAM performed the poorest, both in terms of AIC score (43,703.08) and diagnostics of residuals and overdispersion (Figure S2), and explained 39.3% of the deviance
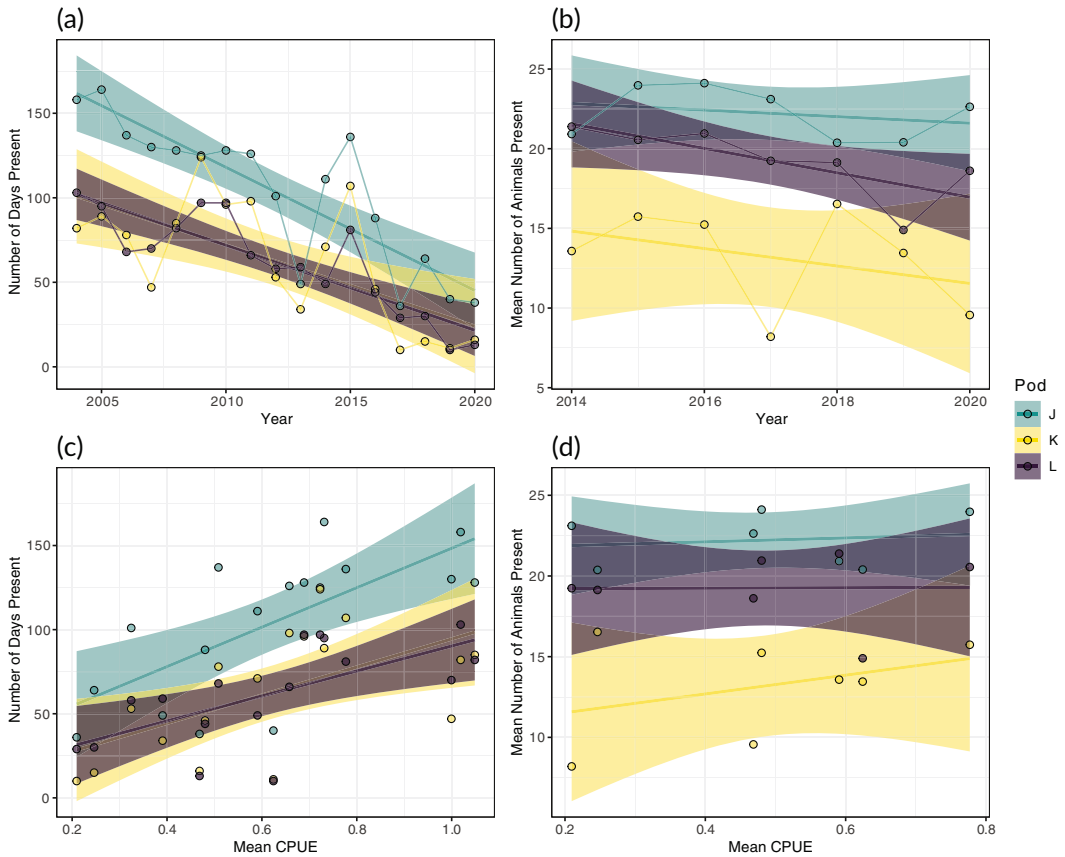
FIGURE 3 Changes in Southern Resident killer whale core summer habitat occupancy. (a) The number of days that any member of J pod (teal), K pod (yellow), or L pod (purple) was recorded in the core summer habitat between April 1 and October 31 each year. (b) The mean number of whales observed on days when each pod was present, by year. (c) The relationship between the number of days each pod was present in core summer habitat and the contemporary annual mean Albion test fishery CPUE. (d) The relationship between the mean number of whales observed on days when each pod was present and contemporary annual mean CPUE. In all panels, the linear model fits are plotted with the standard error of the fit (polygons).
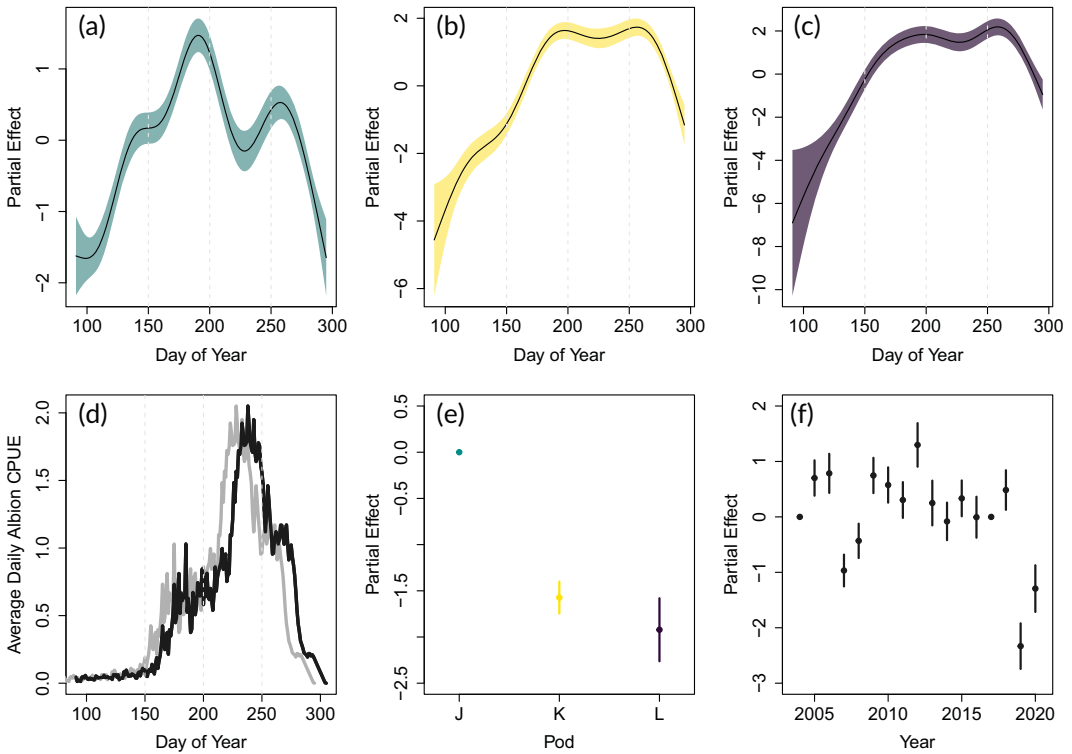
in the count data. We report the effective degrees of freedom for each smooth term for all models in Table S2. The zero-inflated Poisson model (34.8% deviance explained) had a lower AIC score (11,459.97) than the negative binomial model (32.8% deviance explained; AIC 13,553.09), but diagnostics suggested that the negative binomial model better accounted for overdispersion in the data set. The residuals in the negative binomial model were slightly negatively biased, but were far less dispersed than the residuals from either the Poisson or zero-inflated Poisson models, both of which had bimodal residual distributions and were more likely to underpredict observations on the left side of the distribution (Figure S2). Consequently, we selected the negative binomial model as our preferred model for inference.

In our model validations, we found a significant correlation between the observed presence/absence records and the binomial model-predicted presence/absence, and between the observed counts and the negative binomial model-predicted counts using 80% of the data to train the model and 20% of the data to validate the model (Pearson's correlation $p < .001$ in all five validations for both models). For the binomial model, the Wilcoxon rank sum test was significant ($p < .001$) in two of five validations. For the negative binomial count model, the Wilcoxon

TABLE 1 Cetacean sightings as proxies for survey effort 2014–2020. Number of days that each of four cetacean species were reported to JC from any of the sightings sources in the Southern Resident killer whale traditional core summer habitat between April 1 and October 31. The proportion of days with whales is the number of days with any cetacean reported (excluding SRKW) divided by 215. Proportion of days that SRKW were accounted for refers to the number of days SRKW were reported to JC from any sightings sources in any location (not restricted to the core habitat) divided by 215. The proportion of SRKW days in the core habitat refers to the number of days SRKW were reported in the core habitat divided by the number of total days SRKW were accounted for.

| Year	Gray whale	Humpback whale	Minke whale	Transient killer whale	Any cetacean (excluding SRKW)	Proportion of days with whales	Days SRKW reported in core habitat	Days SRKW reported anywhere	Proportion of days SRKW accounted for	Proportion of SRKW days in core habitat
2014	3	80	102	97	183	0.85	119	146	0.68	0.82
2015	4	154	119	103	197	0.92	146	163	0.76	0.90
2016	15	139	102	112	201	0.93	97	130	0.60	0.75
2017	11	146	68	140	201	0.93	53	85	0.40	0.62
2018	9	145	104	146	203	0.94	69	108	0.50	0.64
2019	123	168	130	140	208	0.97	45	86	0.40	0.52
2020	–	–	–	118	–	–	46	80	0.37	0.58

FIGURE 4 Generalized additive model results for the presence of Southern Resident killer whale pods in the core summer habitat (binomial model). The day-of-year partial effect smooth for (a) J pod, (b) K pod, and (c) L pod. (d) The mean daily Albion test fishery Chinook CPUE, averaged across 2004–2020 (black line) and shifted forward by 10 days (gray line) for inclusion in the GAM. The partial effect of pod (e) and year (f) on the probability of presence in the core summer habitat. Shading in a–c and error bars in e–f represents the standard error of the partial effect.

rank sum test was significant ($p < .001$ in all five validations), indicating that while the binomial and negative binomial models are capable of estimating mean trends, the observed data were still overdispersed relative to the modeled distributions.

The negative binomial count model (hereafter simply "count model") found similar patterns from 2014 to 2020 as the binomial model did for the full 2004–2020 study period. There were significant estimated effects of pod, year, day of year, and mean contemporary Albion CPUE for all pods ($p < .01$ in all cases) (Figures 6 and 7). Daily Albion CPUE appears to have had no significant effect for any of the pods (Figure 7). As with the binomial model, the count model estimated J pod to have the highest mean attendance in the traditional core summer habitat, followed by K pod and then L pod. We found no significant difference in the estimated year effect from 2014 to 2018, but 2019 and 2020 both had significantly lower estimated mean attendance ($p < .001$). Attendance of J and K pods peaked from mid-July to late September, whereas attendance of L pod was generally very low until early June, at which point it plateaued for the remainder of the summer season. Mean contemporary Albion CPUE was positively related to the attendance of all three pods.

4 | DISCUSSION

This study adds to a substantial body of work showing that the movements, habitat use, health, and demographic trends of the Southern Resident killer whale population are closely linked to Fraser River Chinook salmon
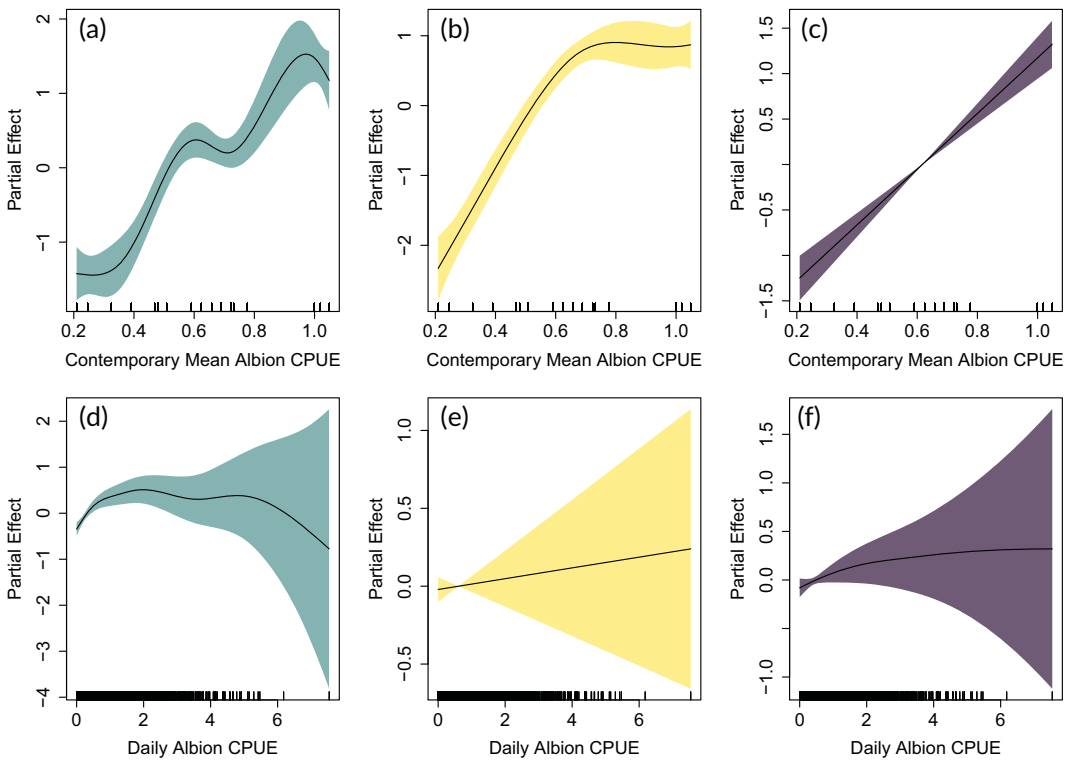
FIGURE 5 Relationships between the probability of Southern Resident killer whale presence in the traditional core summer habitat and Albion test fishery Chinook CPUE (binomial model). The partial effect smooths are shown for the contemporary year mean Albion CPUE and (a) J pod, (b) K pod, and (c) L pod, and for the daily Albion CPUE and (d) J pod, (e) K pod, and (f) L pod. Shading in all panels represents the standard error of the partial effect. Smooth terms in a–d were significant, whereas smooth terms in e–f were not significant (see Results).

abundance. We show that the probability of all three SRKW pods being present in their traditional core summer habitat is related to the average annual Fraser River Chinook returns in the current year. We demonstrate a striking decline in the core summer habitat use by all three SRKW pods, which had an observed occupancy rate of roughly 50%–75% from April 1 to October 31 in the early 2000s, down to an occupancy rate of roughly 5%–15% in recent years, with J pod seen more frequently than K or L pods. Over the same period, average daily Fraser River Chinook CPUE has declined by more than half. While the abundance of the SRKW population also declined from 2004 to 2020, the relative magnitude of that decline is far smaller than the decline in core summer habitat occupancy both overall and at the pod level (Table 2), suggesting that the decline in occupancy is not driven by patterns in SRKW abundance. Our findings corroborate a recent study showing that the phenology of SRKW visitation to the San Juan Islands (within the traditional core summer habitat area) is linked to the timing of Fraser River Chinook returns, and has shifted later in the summer season as spring returns have declined dramatically (Ettinger et al., 2022). The potential impact of declining prey availability on SRKW foraging strategies was highlighted in 2019 and 2020, when despite a modest increase in mean Fraser River Chinook CPUE, SRKW presence in the core summer habitat remained near its minimum level for the study period. This suggests that declining trends in Fraser River Chinook returns may be driving SRKW to forage in other areas outside of the core summer habitat (e.g., in their typical winter range; Hanson et al., 2021) rather than risk encountering low prey densities that they experienced in prior years.

Accounting for survey effort when using many different types of opportunistic and community-contributed survey data is extremely challenging. Our metrics of non-SRKW cetacean sighting days suggest that between 2014 and
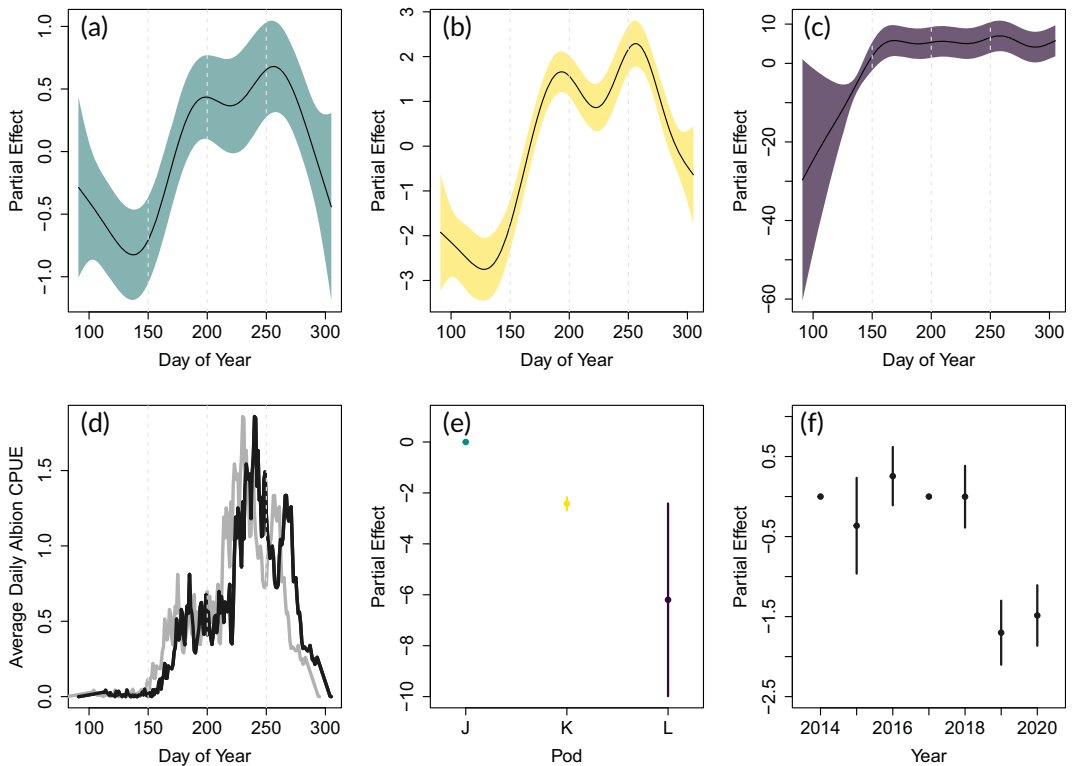
FIGURE 6 Generalized additive model results for the number of Southern Resident killer whales from each pod observed in the traditional core summer habitat (count model). The day-of-year partial effect smooth for (a) J pod, (b) K pod, and (c) L pod. (d) The mean daily Albion test fishery Chinook CPUE, averaged across 2014–2020 (black line) and shifted forward by 10 days (gray line) for inclusion in the GAM. The partial effect of pod (e) and year (f) on the number of whales observed per day in the core summer habitat. Shading in a–c and error bars in e–f represents the standard error of the partial effect.

2020, the same sources that provided SRKW sightings reports, both from shore, research vessels, and commercial whale watching operations, were active and submitting cetacean sightings on average more than 90% of the April–October study period. In addition, our SRKW sightings from outside of the core summer habitat indicate that SRKW whereabouts were known for, in some cases, almost twice as many days as their reported presence in the core habitat. This suggests that for the 2014–2020 period, our sightings data approach true presence/absence of SRKW in the core summer habitat, rather than days without sightings simply reflecting a lack of survey effort. For the 2004–2013 study period, we do not have similar non-SRKW cetacean sightings to quantify relative survey effort. Survey effort during this early period may have been lower than the 2014–2020 period as there were fewer whale watching operations and researchers compared to recent years, although we note that in 2004 and 2005 we have SRKW sighting reports from more than 75% of the days in the April–October study period. If survey effort was lower in early years and increased over time, with more false SRKW absences in early years than in later years, the decline in core habitat occupancy that we report would in fact be underestimated. In addition, the negative binomial distribution we used in our count model should account for overdispersion in the sightings data, which could be caused in part by false absences.

With very few exceptions, J pod spent the most time in the traditional core summer habitat each year, and more J pod whales were present on average in the core habitat than any other pod, despite L pod being about 50% larger numerically than J pod. From 2014 to 2020 when individual-level data were available for each pod, virtually all of J
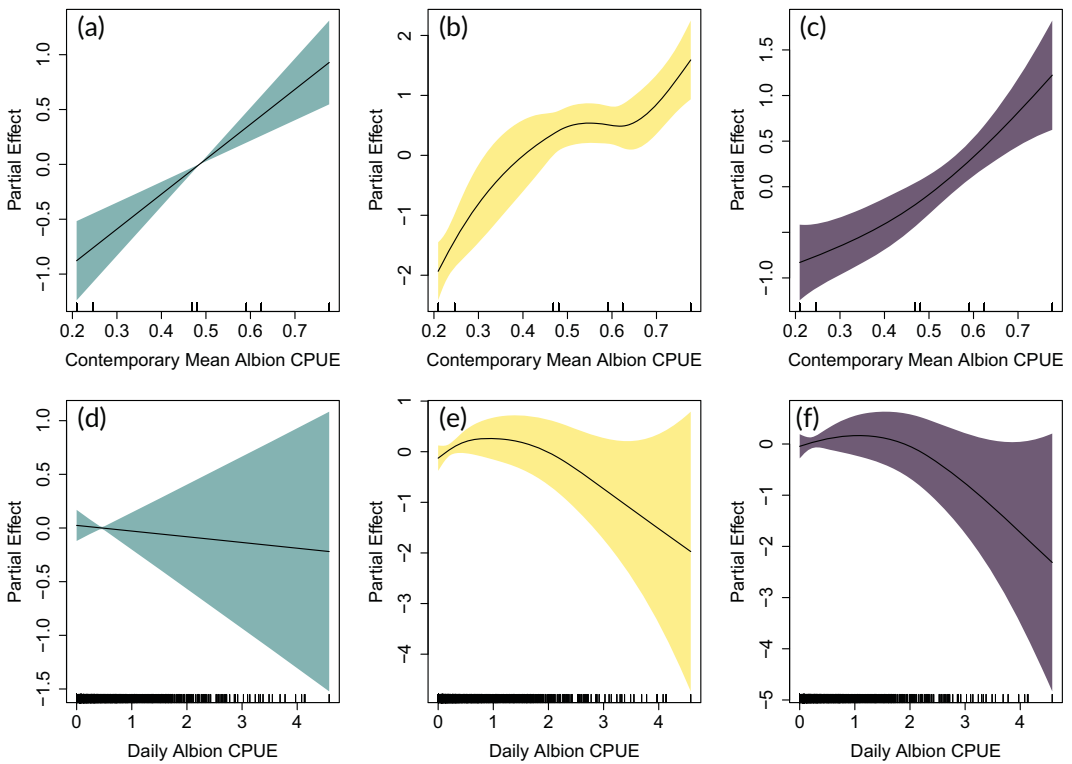
FIGURE 7 Relationships between the number of Southern Resident killer whales observed in the traditional core summer habitat and mean annual Albion test fishery Chinook CPUE (count model). The partial effect smooths are shown for the contemporary year mean Albion CPUE and (a) J pod, (b) K pod, and (c) L pod, and for the daily Albion CPUE and (d) J pod, (e) K pod, and (f) L pod. Shading in all panels represents the standard error of the partial effect. Smooth terms in a–c were significant, whereas smooth terms in d–f were not significant (see Results).

pod was present on days when the pod was observed, whereas roughly two-thirds of K and L pods were typically present on average when those pods were observed. These findings align with previous studies indicating that K and L pods use the outer coast of Washington, Oregon, and California more extensively than J pod (Hanson et al., 2013, 2017), and a recent study showing that J pod body condition was closely related to Fraser River Chinook at-sea abundance (Stewart et al., 2021), whereas L pod body condition was best explained by Puget Sound Chinook salmon and K pod body condition had no clear relationship to the abundance of a specific Chinook stock. Collectively these studies suggest that the three SRKW pods may target somewhat distinct but overlapping prey sources throughout the year, resulting in pod-specific spatiotemporal distributions throughout their range. However, we note that although K and L pods spent fewer days in the core summer habitat than J pod on average, all three pods showed relationships between presence in the region and mean Fraser River Chinook returns. J pod has also exhibited the greatest shift in peak occurrence in the San Juan Islands in step with the shifting peak daily returns of Fraser River Chinook (Ettinger et al., 2022), further suggesting that J pod's use of the SRKW core summer habitat may be most closely related to this Chinook stock. This suggests that while Fraser River Chinook may be an important diet item for all three pods, J pod may be impacted most by declining Fraser returns.

While we did not explicitly examine changes in the timing of SRKW visitation throughout the study period, the modest differences in the seasonal (day of year) smooths in the GAM analyses between the presence/absence GAM for 2004–2020 (Figure 4a–c) and the count-based GAM for 2014–2020 (Figure 6a–c) mirror the phenological shifts described in Ettinger et al. (2022). J pod peak attendance shifted slightly later in the summer in the 2014–2020

TABLE 2 Sighting rates of Southern Resident killer whales in the traditional core summer habitat 2004–2020. The July census is the total abundance of each pod as of July 1 in each year. Note that the mean number of whales present can be higher than census abundance due to births and/or deaths prior to/after the census. Occupancy proportion is the number of days each pod was present divided by 215 (the number of days present between April 1 and October 31).

	J pod					K pod					L pod					Days any SRKW present
	July census	Days present	Occupancy proportion	Animals present		July census	Days present	Occupancy proportion	Animals present		July census	Days present	Occupancy proportion	Animals present		
Year				Mean	SD				Mean	SD				Mean	SD	
2004	22	158	0.73	–	–	20	82	0.38	–	–	41	103	0.48	–	–	162
2005	23	164	0.76	–	–	21	89	0.41	–	–	44	95	0.44	–	–	168
2006	24	137	0.64	–	–	21	78	0.36	–	–	44	68	0.32	–	–	140
2007	25	130	0.60	–	–	19	47	0.22	–	–	42	70	0.33	–	–	136
2008	25	128	0.60	–	–	19	85	0.40	–	–	41	82	0.38	–	–	142
2009	26	125	0.58	–	–	19	124	0.58	–	–	40	97	0.45	–	–	143
2010	28	128	0.60	–	–	19	96	0.45	–	–	39	97	0.45	–	–	132
2011	26	126	0.59	–	–	19	98	0.46	–	–	42	66	0.31	–	–	133
2012	25	101	0.47	–	–	19	53	0.25	–	–	40	58	0.27	–	–	103
2013	26	49	0.23	–	–	19	34	0.16	–	–	37	59	0.27	–	–	78
2014	25	111	0.52	20.92	5.95	19	71	0.33	13.58	6.96	34	49	0.23	21.39	5.64	116
2015	27	136	0.63	23.98	6.66	19	107	0.50	15.74	5.09	35	81	0.38	20.56	9.40	145
2016	29	88	0.41	24.11	7.88	19	46	0.21	15.24	4.93	35	44	0.20	20.95	9.07	96
2017	24	36	0.17	23.11	2.97	18	10	0.05	8.20	6.76	35	29	0.13	19.24	8.71	51
2018	23	64	0.30	20.38	5.20	18	15	0.07	16.53	4.16	34	30	0.14	19.13	4.51	68
2019	22	40	0.19	20.40	4.11	17	11	0.05	13.45	4.74	34	10	0.05	14.90	8.01	44
2020	22	38	0.18	22.63	0.82	17	16	0.07	9.56	5.74	33	13	0.06	18.62	5.91	46

analysis compared to the 2004–2020 analysis, K pod attendance remained largely the same, and L pod attendance peaked (and plateaued) slightly earlier in the season.

We found no clear relationships between the daily CPUE reported in the Albion test fishery (moved forward by 10 days) and SRKW presence or abundance in the traditional core summer habitat. It is possible that our selection of a 10-day lead period was inadequate to capture the migratory period of a salmon between the SRKW core summer habitat and the Albion test fishery, although we did explore a range of leads from 0 to 21 days, all of which had similarly nonsignificant relationships between SRKW attendance and daily Albion CPUE. We suggest that a more likely explanation is that SRKW are not responding to prey availability at such fine (i.e., daily) timescales, but are instead responding to seasonal patterns in Chinook returns, as suggested by Ettinger et al. (2022). Further, if daily Chinook returns are generally high but have periods of low abundance between pulses, this overall prey availability may be sufficient for SRKW to remain within the core summer habitat but may obscure estimated relationships with daily returns and be better reflected in average returns, as indicated by our model results. Our GAM analyses showed similar patterns, regardless of whether the data were binomial presence/absence records or counts of individual whales. Given the relative consistency in the mean number of whales typically observed in the core summer habitat (Figure 3), most of the information content in our analyses is contained in the presence or absence of whales rather than the recorded daily abundance. It would be reasonable to predict that not only the probability of visitation in the core summer habitat, but also the number of whales present on a given day, would decline with decreasing prey availability. However, given the strong social foraging behaviors exhibited by SRKW pods and matrilines, it is perhaps unsurprising that we did not find any clear decline in the average number of whales recorded on days that they accessed the core summer habitat.

Several recent studies have suggested that prey availability during the winter foraging period may be most relevant to SRKW population health and dynamics, given that their preferred Chinook prey are more dispersed and make up a smaller portion of their diet (Ford et al., 2016; Hanson et al., 2010, 2021; Wasser et al., 2017). Consequently, perturbations to their food supply in winter months could have greater consequences for fitness, survival, and fecundity than similar perturbations to summer prey stocks. However, given the reported seasonal decline in SRKW body condition when comparing late summer (September) to late spring (May) (Fearnbach et al., 2020), the availability and abundance of summer prey may be critical to building blubber stores that facilitate survival through the winter period when prey availability is low. Our findings suggest that SRKW are facing increasing challenges to finding and capturing adequate prey in the core summer habitat during this important feeding period, and may be foraging in other locations instead. Furthermore, given the comparatively high energetic content of Fraser River Chinook (O'Neill et al., 2014), it may be difficult for SRKW to compensate for the decline in Fraser Chinook availability by foraging in other locations and on other salmon stocks and species during the summer months. Increasing Fraser River Chinook abundance is not necessarily straightforward, as climate change (Crozier et al., 2008) and upstream habitat degradation (Greene & Beechie, 2004) are thought to be major threats to Fraser Chinook stocks, both of which are challenging to address with short-term management interventions. In addition, hatchery supplementation of wild stocks in the Fraser River tributaries is minimal compared to other tributaries (Hanson et al., 2021). Reductions in the take of Fraser River Chinook stocks could increase their availability to SRKW during this important summer feeding period. Given the decline in traditional core summer habitat use over the past two decades that we report here, it will be important for future studies to evaluate if and how the summer diets of SRKW have changed over this period, and if the population is able to meet its energetic demands by supplementing its summer diet with other prey species or Chinook salmon stocks found outside of the central Salish Sea. Given the major decline in Fraser River Chinook returns, reducing disturbance of the SRKW population within their traditional summer foraging grounds may be critical in order to maximize foraging efficiency during the truncated period that they now occupy the Salish Sea.

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AUTHOR CONTRIBUTIONS

Joshua D. Stewart: Conceptualization; formal analysis; investigation; methodology; supervision; visualization; writing – original draft; writing – review and editing. **Jane Cogan:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing – review and editing. **John W. Durban:** Conceptualization; funding acquisition; investigation; project administration; writing – review and editing. **Holly Fearnbach:** Conceptualization; funding acquisition; investigation; project administration; writing – review and editing. **David K. Ellifrit:** Investigation; methodology; resources; writing – review and editing. **Mark Malleson:** Investigation; methodology; resources; writing – review and editing. **Melisa Pinnow:** Data curation; investigation; methodology; resources; writing – review and editing. **Kenneth C. Balcomb:** Conceptualization; data curation; funding acquisition; investigation; methodology; resources; writing – review and editing.

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