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ARTICLE

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The diverse diet of southern Alaska resident killer whales shifts across spatiotemporally distinct foraging hotspots

Hannah J. Myers[1] | **Daniel W. Olsen**[2] | **Amy M. Van Cise**[3] | **Abigail H. Wells**[4,5] | **Kim M. Parsons**[6] | **Craig O. Matkin**[2]

[1]College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, Alaska, USA

[2]North Gulf Oceanic Society, Homer, Alaska, USA

[3]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington, USA

[4]Lynker Technologies, Leesburg, Virginia, USA

[5]Under contract to Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington, USA

[6]Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington, USA

Correspondence
Kim M. Parsons
Email: kim.parsons@noaa.gov

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Abstract

Top predators influence ecological communities in part through the prey they consume. Prey preferences often shift throughout the year, reflecting both seasonal and geographic patterns of habitat use and the relative abundance of preferred prey species. Killer whales (*Orcinus orca*) are top predators in the marine ecosystem, and understanding their diet is critical to assess their ecological impacts and role. In this study, we examine the diet of the southern Alaska resident killer whale population across three major foraging hotspots. We leverage two complementary sampling methods—morphological ID and genetic metabarcoding—to reveal strong spatiotemporal patterns in diet from May through September. Chinook, chum, and coho salmon were each important prey resources in different locations and times, with consistent dietary contributions from Pacific halibut, arrowtooth flounder, and sablefish. Our results reveal a diverse, location-specific, and strongly seasonal foraging strategy in this top predator and highlight the increased resolution provided by using ensemble techniques to characterize foraging behavior. Effective conservation and management of this population will depend on broad spatiotemporal sampling to accurately characterize foraging ecology.

KEYWORDS
diet composition, foraging ecology, groundfish, killer whale, salmon, top predator

INTRODUCTION

The foraging ecology of top predators reflects complex predator–prey dynamics. Top predators influence ecological communities in part by affecting the abundance and behavior of prey species they consume. Conversely, the distribution and abundance of predators are influenced by the availability of prey. Many predators track prey resources over time according to their abundance, timing, ephemerality, and predictability, among other factors (Abrahms et al., 2021), resulting in pronounced seasonal patterns in foraging strategies. Within populations, individuals and family or social groups often further develop

Hannah J. Myers and Daniel W. Olson contributed equally to the work reported here.

specialized foraging strategies (Deacy et al., 2018; Durban et al., 2023; Stanek et al., 2017; Teixeira et al., 2023; Whitehead & Ford, 2018). Understanding changes in predator diet across time, space, and among conspecifics is therefore critical to assessing how prey variability influences predator ecology.

Killer whales (*Orcinus orca*) are top predators in the marine ecosystem and are most abundant in high-latitude regions (Forney & Wade, 2006). In the North Pacific, killer whale lineages have diverged into three distinct ecotypes: those that exclusively eat fish (known as residents), those that exclusively eat mammals (known as transients or Bigg's), and those that consume mostly sharks (known as offshores) (Ford et al., 2011, 2014; Wright et al., 2025). The fish-eating "resident" type, newly recognized as a divergent subspecies (*O. o. ater*; Morin et al., 2024), is most abundant, with at least four parapatric populations spanning coastal regions in the northeast Pacific (Bigg et al., 1990; Parsons et al., 2013). The 74 animals in the critically endangered southern resident population are primarily found from southern British Columbia to California (Carretta et al., 2023). The northern resident population of an estimated 341 individuals is found primarily off the coasts of British Columbia and southeast Alaska (Department of Fisheries and Oceans, 2022). The southern Alaska resident population of about 1000 killer whales ranges from southeast Alaska to Kodiak Island (Matkin et al., 2014). Finally, there are at least 1000 animals in the Alaska resident North Pacific stock west of Kodiak Island and north into the Bering Sea (Young et al., 2023).

Pacific salmon (*Oncorhynchus* spp.) are important prey for all studied North Pacific fish-eating killer whale populations. Southern residents, in particular, feed almost exclusively on Chinook salmon (*Oncorhynchus tshawytscha*) in spring and summer—though their diet is significantly more diverse in fall and winter (Hanson et al., 2021). Northern residents forage mostly for Chinook salmon and, to a lesser extent, chum salmon (*Oncorhynchus keta*) (Ford & Ellis, 2006) in summer. Southern Alaska residents eat substantial portions of Chinook, chum, and coho salmon (*Oncorhynchus kisutch*) (Saulitis et al., 2000; Van Cise et al., 2024). Western Alaska North Pacific residents are less well studied but may consume lower trophic level fish farther west where salmon are less available (Krahn et al., 2007), and at least some pods depredate groundfish species from commercial longline and trawl fisheries (Peterson et al., 2013; Dahlheim et al., 2022). On the other side of the Pacific, fish-eating killer whales in Avacha Gulf eat mostly coho salmon, chum salmon, and Atka mackerel (*Pleurogrammus monopterygius*) in summer (Tarasyan et al., 2005; Volkova et al., 2019).

While the importance of salmon as prey for North Pacific fish-eating killer whales is well established, how these animals utilize different prey resources across space and time is less understood—especially for the substantially larger populations found off Alaska. In this study, we take advantage of a long-term killer whale monitoring program to examine how the diet of southern Alaska resident killer whales changes across three main foraging hotspots occurring during summer months. We use both prey (scale and flesh) samples and predator fecal samples to characterize the relative importance of different prey species. This work adds to our understanding of prey selection by fish-eating killer whales, providing valuable insight into their spatiotemporal foraging strategies and the potential ecological impacts of prey variability on predator distribution.

METHODS

Sample collection

Fieldwork took place between May and September in Prince William Sound and Kenai Fjords, Alaska, USA (Figure 1), under National Marine Fisheries Service research permits numbers 782-1719, 545-1488, 15616, and 20341. Fieldwork location and timing were informed by prior knowledge of hotspots based on success rates of encountering killer whales during long-term vessel-based field research in this region. Southern Alaska resident killer whales display seasonal and pod-specific differences in core use areas within this region (Olsen et al., 2018). Prey samples were collected from 1991 to 2021, and fecal samples were collected from 2016 to 2021. Prince William Sound is characterized by large barrier islands, entrances with strong tidal currents, and small islands scattered near glacially carved trenches. Kenai Fjords run along the southern Alaska coast and have many long glacially carved fjords.

All fieldwork was conducted from an 11-m research vessel concurrent with other research tasks including photo-identification, acoustic research, and body condition assessment. Prey and fecal samples were collected from surface waters during focal follows of resident killer whale groups. Prey capture attempts were typically identified when killer whales made tight turns or lunges at the surface and/or when a whale approached to share a fish, often with its mother (Ford & Ellis, 2006; Saulitis et al., 2000; Wright et al., 2016). When a likely prey capture attempt was observed, the site was approached quickly to search for scales or pieces of prey tissue in the water, while taking care to avoid disturbing the animals. Fecal samples were usually found in fluke print

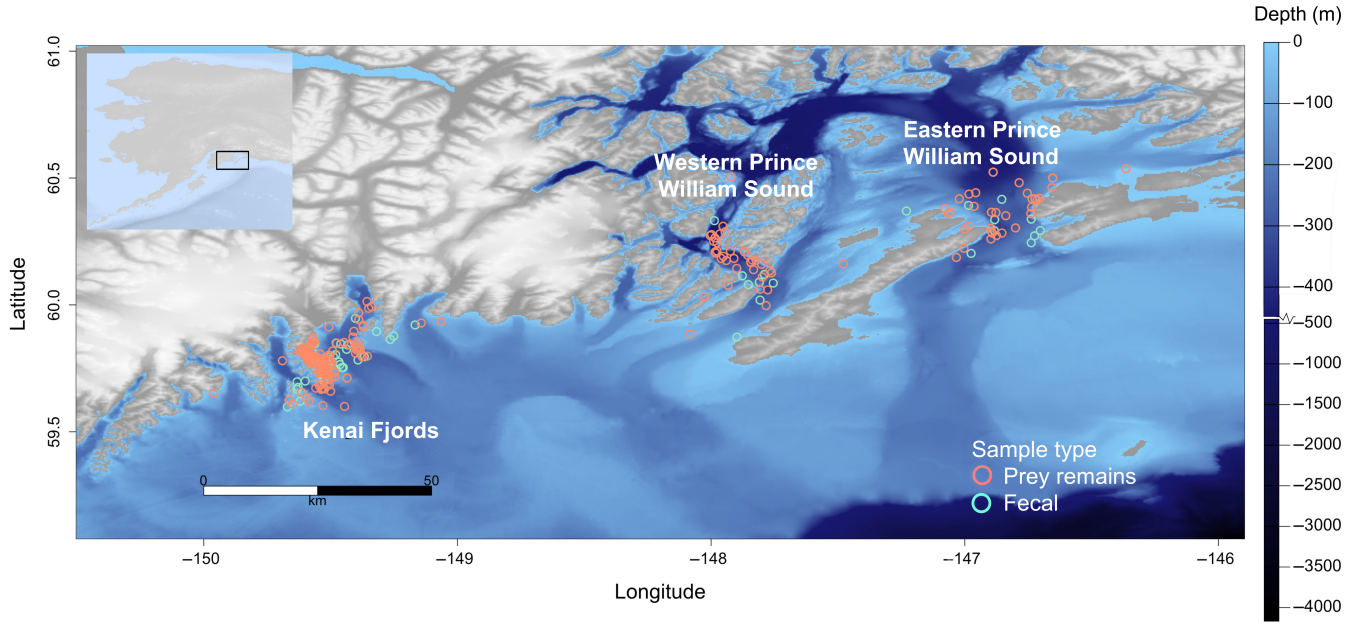

FIGURE 1 Map of prey remains and fecal samples collected in the study area in the northern Gulf of Alaska. Coordinates were not available for all prey samples collected prior to 2009 (primarily collected in western Prince William Sound); samples without coordinates were matched to foraging hotspots but not included in this figure. The inset map shows the study area in the northern Gulf of Alaska.

upwellings (upward currents from the flukes of a diving whale) while the vessel was traveling >100 m behind the whales.

Samples were collected from the bow using a long-handled fine-mesh dip net and transferred into new glass jars. All samples were labeled and frozen within 10 min of collection; prey samples were frozen in ethanol. Dip nets were sterilized with a bleach/seawater solution between sampling events. Previous research has demonstrated that samples collected from seawater have minimal DNA contamination from seawater (Apprill et al., 2011, 2014; Bik et al., 2016).

The identity of individual killer whales and pods encountered was determined using photo-identification. Identification photos were taken with a Nikon D700 or D750 camera with a 200-, 300-, or 400-mm lens and matched to a long-term photo-identification catalog maintained by the North Gulf Oceanic Society (North Gulf Oceanic Society, 2023). In each encounter, all members of a matriline (defined as a mother or grandmother and her offspring) were assumed to be present if at least one member of the matriline was photographed, as in Olsen et al. (2020) and Myers, Olsen, Konar, et al. (2025). We documented the individual or pod from which each sample was collected when possible. However, in multi-pod encounters, this was not always feasible because the animal involved in prey capture or fecal sampling was not always viewed from an angle that enabled identification during the sampling event. Killer whale fecal samples were genotyped using an established and validated multilocus SNP panel (Hanson et al., 2021; Van Cise et al., 2024) to identify fecal samples originating from the same host whale (see below for details on DNA extraction methods).

Identifying prey sample pseudoreplicates was therefore challenging because it was often not possible to determine which individual animal or pod captured the fish that was sampled. However, we conducted a sensitivity analysis to assess how removing different levels of potential pseudoreplicates may affect prey sample results (details in Appendix S1). In this analysis, we removed potential pseudoreplicated samples that were collected from the same group of animals within 1 or 2 h of each other and then conducted the same statistical analysis and compared it with results from the full dataset.

Prey species identification

Prey samples

Salmonid prey samples were identified to species by experts at the Schlerochronology Laboratory (Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, BC) using fish scale morphological characteristics (MacLellan, 2004; McNicol & MacLellan, 2010; MacLellan & Gillespie, 2015). If scales could not be positively assigned to a species in this manner, or if only

tissue fragments were collected from a killer whale predation event, the salmon species was identified using genetic techniques (either microsatellite or single-nucleotide polymorphism markers, depending on the year the sample was collected). Genetic analysis was conducted by the Molecular Genetics Laboratory (Pacific Biological Station, Fisheries and Oceans Canada), following methods described by Withler et al. (2004) for microsatellites and, more recently, by Beacham and Wallace (2020) for single-nucleotide polymorphism markers. Scales were dried for schlerochronology; otherwise, scales and tissues were preserved in 90% ethanol.

Fecal sample prey metabarcoding

Whole genomic DNA was extracted from a pea-sized subsample of frozen fecal matter using the QIAamp Fast DNA Stool mini kit following standard protocols executed using the QIAcube automated extraction robot (Ford et al., 2016). Using custom-designed Illumina primers for salmon and groundfish, 16S SSU rDNA was targeted as previously published for the prey metabarcoding of southern resident killer whales (Ford et al., 2016). Amplification reactions contained 4 μL of DNA, 1X Promega GoTaq Flexi buffer (Promega, Madison, WI), 3.0-mM MgCl2, 0.2 mM of each dNTP, 0.1 μg/μL of BSA, 0.2 μM of each primer, and two units of Promega GoTaq Flexi DNA Polymerase. Prey DNA was amplified in a 32-cycle PCR, with cycling conditions as follows: initial denaturation at 94°C for 2 min, followed by 32 cycles of 94°C for 35 s, 61°C for 1 min, 72°C for 35 s, and a final extension at 72°C for 5 min. Amplicons were gel cleaned using Qiagen MinElute columns to remove nontarget PCR products and primer dimer.

Cleaned amplicons were individually indexed using two different sets of indices. In 2018 and 2019, Illumina Nextera forward and reverse index tags were used, which create a unique combination of indices by using a unique forward primer for each column and a unique reverse primer for each row on a 96-well plate. This indexing PCR was completed using a 50-μL reaction containing 8 μL of gel purified PCR product, 1X NEB Phusion High-Fidelity master mix (New England BioLabs), 0.2 mM of each dNTP, and 5 μL each of one Illumina Nextera forward and reverse index tag. In the two 2021 MiSeq runs, Illumina Nextera DNA Unique Dual Index (UDI) primers were used, comprising unique forward and reverse indexes for each well in a 96-well plate in order to reduce the effect of index hopping (Kircher et al., 2012). The index PCR was performed in a 40-μL reaction containing 8 μL of gel purified PCR product, 1.25 μL of Illumina Nextera UDI index or 1 μL each of the forward and reverse Illumina combinatorial indexes, and 30 μL of Phusion High-Fidelity PCR Master Mix (New England Biolabs). Regardless of the indices used, the indexing PCR conditions remained the same: 72°C for 3 min, 98°C for 30 s, followed by 12 cycles of 98°C for 10 s, 55°C for 30 s, 72°C for 30 s, and a final extension at 72°C for 5 min. Samples were sequenced on four sequencing runs (2018, 2019, and two in 2021) using an Illumina MiSeq next generation sequencer at the Northwest Fisheries Science Center, NOAA Fisheries, Seattle, WA.

In addition to fecal samples from southern Alaska resident killer whales, two mock communities comprising known quantities of genomic DNA from several vouchered fish species were included on each of the four sequencing runs to detect and control for any potential bias caused by index hopping or species-specific amplification efficiency. Details on mock community generation can be found in Van Cise et al. (2024). Mock communities were sequenced alongside sample libraries each year.

Fecal sample prey metabarcoding sequence analysis

Sequences from all runs were combined and analyzed using a custom pipeline based on the dada2 package (Callahan et al., 2017) in the R computing environment (R Core Team, 2024). This pipeline includes steps for (1) trimming sequences based on general sequence quality, (2) filtering sequences based on a maximum number of expected errors (Edgar & Flyvbjerg, 2015), (3) learning the error rates for each possible transition, (4) de-replicating sequences by combining and counting identical sequencing reads to reduce computation time, and finally inferring unique amplicon sequence variants (ASVs) from the filtered and trimmed sequences using the previously learned error rates (Callahan et al., 2017). Once unique ASVs were identified, paired forward and reverse reads were merged and chimeras removed. Taxonomy was assigned to the remaining ASVs using a naïve Bayesian classifier (Wang et al., 2007) that relies on a fasta-formatted reference database, which we custom-generated by downloading sequences for all fish and shark species from NCBI GenBank.

Because various sources of laboratory-introduced bias can affect the observed number of reads assigned to a given species, mock community control samples were used to estimate and correct for the effects of errors, for example, from amplification bias and index hopping. This model was run using both mock communities to estimate species-specific bias, and read proportions by species were corrected based on model estimates (Van Cise et al., 2024: Figure 2). Some prey species in the final

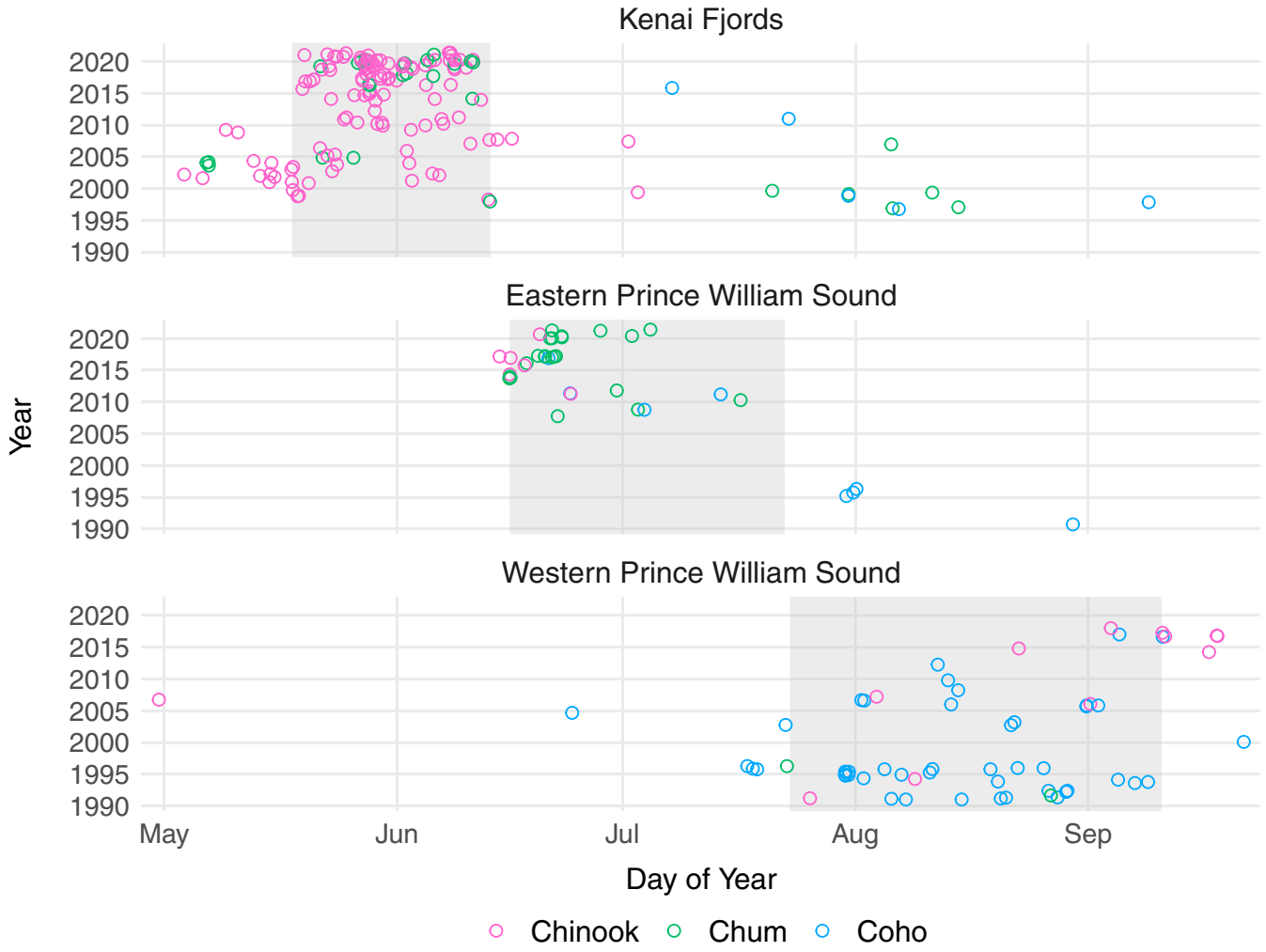

FIGURE 2 Samples of prey remains collected from each area from May through September across all years. Gray shaded periods indicate the days during which 80% of prey samples were collected in each area.

dataset were not anticipated, for example, sablefish, and therefore not included in the mock communities and could not be corrected. However, overall differences between uncorrected and corrected proportional data are small enough that the difference for these species is expected to be minor (Van Cise et al., 2024; Appendix S1: Figures S3 and S4).

Final data filtering consisted of removing ASVs that were assigned to *Orcinus orca* and aggregating ASVs by species. Laboratory and field duplicates used to track potential sources of bias or contamination were removed from the dataset before analysis. Additionally, samples with a read depth <25,000 reads were excluded to ensure all samples are within an order of magnitude of sampling depth, thus avoiding sampling bias, following methods in (Van Cise et al., 2024). Additionally, individual whale ID was genetically determined using a previously developed panel of SNPs (see Van Cise et al. (2024) for methodological details), and samples were removed if they were collected from the same individual on the same day to avoid pseudoreplication. Prey species were only included in downstream analyses if they represented >1% of the reads in one or more samples in the dataset to avoid potential bias from sequencing error.

Statistical analyses

We modeled the effect of foraging hotspot on prey species composition with Bayesian multinomial regression models. For prey samples, we used a multinomial logistic regression; for fecal samples, we used a Dirichlet-multinomial distribution to handle the proportional nature of the data. Models were implemented using the *brms* package (Bürkner, 2017) in R (version 4.3.3) with the default uninformative priors. We expected the foraging hotspot area (a three-level categorical variable) to be highly correlated with the day of year and the year in which the sample was

collected because our field effort was seasonally concentrated first in Kenai Fjords, then eastern Prince William Sound, and then western Prince William Sound, and we worked in western Prince William Sound less often in later years (Appendix S1: Figures S1 and S2). We evaluated the pairwise correlations between hotspot area, day of year, and pod using the *polycor* package in R (Fox, 2022). We then tested separate models that included either the effect of hotspot area or a smooth function of day of year and compared them using expected log predictive density (ELPD) implemented using the *loo* package in R (Vehtari et al., 2017). We did not include both hotspot area and day of year in any model because they were confounded due to sampling effort. We also did not include the effect of year in any models because a potential effect of year was most likely related to shifts in our sampling effort rather than a reflection of changing killer whale diet (Appendix S1: Figure S2).

Once the best model with all data was selected, we made subsets of the data to include only samples for which the pod involved in the sampling event was documented. Using the subset of the data, we then added a random effect of pod to the best model structure identified in the previous step and used ELPD to determine whether it improved the model.

RESULTS

We collected 255 samples of prey remains (fish scales or flesh) while southern Alaska resident killer whales were observed feeding across 31 years (1991–2021). In addition, we collected 162 fecal samples across 6 years (2016–2021), of which 87 were sequenced successfully, were determined to be independent samples (i.e., not collected from the same individual on the same day), and passed the quality check. All prey and fecal samples were collected in three geographically distinct foraging areas with largely nonoverlapping data collection periods, which we termed "foraging hotspots": Kenai Fjords from mid-May to mid-June, eastern Prince William Sound from mid-June to July, and western Prince William Sound from July through September (Figure 1). Both prey remains (scale and flesh) and fecal samples demonstrated distinct dietary patterns across these three foraging hotspots. Chinook and chum salmon were the predominant species across all diet samples, although coho salmon were the most common prey remains collected in western Prince William Sound. Fecal samples also revealed substantial contributions from Pacific halibut (*Hippoglossus stenolepis*), arrowtooth flounder (*Atheresthes stomias*), and sablefish (*Anoplopoma fimbria*).

Prey remains

Of the 255 scale and flesh samples we collected, 249 originated from three salmon species: Chinook, chum, and coho—each of which was predominant in a different foraging hotspot (Table 1, Figure 2). Only one prey sample did not clearly align with a hotspot area and was therefore removed from the analysis (chum salmon collected on September 4, 2020, at 59.788° N, 148.705° W). We identified the pod involved in 217 prey sampling events. A sensitivity analysis investigating the potential influence of pseudoreplication on prey sample results revealed no notable effect (Appendix S1: Tables S1 and S2); we therefore present the analysis including all prey samples.

Chinook salmon made up 77% of prey samples collected in Kenai Fjords—where 80% of samples were collected between May 17 and June 12. Chum salmon were the primary prey species in eastern Prince William Sound (62% of samples), where sampling took place primarily from June 15 to July 22. Coho salmon dominated the western Prince William Sound foraging hotspot (77%), where we collected samples primarily from July 22 to September 10. In addition to the three main salmon prey species, five sockeye salmon (*Oncorhynchus nerka*) prey samples were collected in May and June in Kenai Fjords and eastern Prince William Sound, and one Pacific herring (*Clupea pallasii*) sample was collected in early May in Kenai Fjords. The main pods (maternally related family groups)—which we defined as those from which at least 10% of samples were collected—differed across the foraging hotspots, although multiple samples were collected from the AK2 pod across all three (Table 1). Pod-specific diet patterns are discussed below.

Hotspot area and day of year were highly correlated (0.82, $s = 0.02$), though the pod from which the sample was collected was not strongly correlated with either spatiotemporal variable (−0.01–0. 05, $s = 0.06$, respectively). Bayesian multinomial logistic regression model results reinforced the statistical significance of the diet patterns described above (Table 2, Figure 3). The model with day of year performed slightly better than the model with hotspot area (ΔELPD $= -19.8$, $s = 10.0$), though the SE of the difference was less than twice ΔELPD and thus only marginally meaningful (Vehtari et al., 2017). We therefore report results from both models (Table 2, Figure 3). Coefficients and hyperparameters for which the 95% credible interval (CI) does not include zero may be interpreted as statistically significant. The day of year model provided clear evidence that prey species varied seasonally in a nonlinear fashion. In the hotspot area model, the quadratic effect of chum salmon reflected the high probability of chum salmon in eastern Prince William Sound, and the strong linear effect of coho

TABLE 1 Samples of prey remains (fish scales and flesh) from three primary salmon prey species, collected while killer whales were observed feeding.

Area	Total samples	Sampling period (80%/all)	Main pods (*n*)	Salmon species	Proportion of samples
Kenai Fjords	149	May 17–Jun 12/May 3–Sep 8	AD8 (41), AD5 (27), AD16 (17), AK2 (17)	**Chinook**	**0.78**
				Chum	0.19
				Coho	0.03
Eastern Prince William Sound	37	Jun 15–Jul 21/Jun 14–Aug 29	AB (7), AD8 (4), AK2 (4), AI (3)	Chinook	0.16
				Chum	**0.62**
				Coho	0.22
Western Prince William Sound	62	Jul 22–Sep 9/Apr 29–Sep 21	AE (23), AB (7)	Chinook	0.19
				Chum	0.03
				Coho	**0.77**

Note: The period within which 80% of samples of prey remains were collected and the range of dates within which all prey samples were collected are shown for each area. The main pods are those from which at least 10% of samples were collected, with the number of samples from that pod in parentheses. Pod was not identified in all sample collections. The predominant prey species from each foraging hotspot is shown in boldface.

TABLE 2 Results from two multinomial logistic regression models showing the probability of Chinook, chum, and coho salmon prey sample remains.

Model	Species	Coefficient/ hyperparameter	Estimate	Lower 95% credible interval	Upper 95% credible interval
Day of year	Chum salmon	Smoothing spline	**7.10**	**2.92**	**14.52**
		Intercept	**−0.87**	**−1.35**	**−0.43**
	Coho salmon	Smoothing spline	**7.37**	**3.58**	**14.87**
		Intercept	**−3.07**	**−5.18**	**−1.69**
Hotspot area	Chum salmon	Intercept	**−0.66**	**−1.36**	**−0.06**
		Linear	−0.39	−1.72	0.65
		Quadratic	**−2.55**	**−3.66**	**−1.59**
	Coho salmon	Intercept	−0.49	−1.03	0.04
		Linear	**3.28**	**2.55**	**4.12**
		Quadratic	−0.99	−2.01	0.01

Note: Estimates of regression coefficients (for intercepts, linear, and quadratic effects) and smoothing spline hyperparameters are shown with 95% credible intervals; estimates for which the 95% credible interval does not include zero are shown in boldface. The model reference level is Chinook salmon. In the hotspot area model, the linear term describes the relationship across the three ordered areas: Kenai Fjords, eastern Prince William Sound, and western Prince William Sound. The quadratic term reflects how the middle level (eastern Prince William Sound) differs from the expected linear relationship between the first (Kenai Fjords) and last (western Prince William Sound) levels.

salmon reflected the higher probability of coho salmon in western Prince William Sound, relative to Chinook salmon. Posterior predictive checks indicated close model fit to observations (Appendix S1: Figure S3), and $\widehat{R}$ was 1.00 for all parameters in both models, suggesting model convergence.

Including the random effect of pod slightly improved model predictions relative to the model with day of year only ($\Delta\text{ELPD} = -8.5$, $s = 4.4$). The variation among pods in the probability of chum salmon prey (relative to Chinook) was relatively small; the SD of the random intercept for chum salmon was 0.48 with a 95% CI of 0.03–1.33. In contrast, pods varied more in the probability of coho salmon prey; the SD of the random intercept for coho salmon was 2.02 (95% CI 0.87–3.86).

Fecal samples

Results from 87 fecal samples reinforced the primary importance of salmonids in the diet of southern Alaska resident killer whales while also revealing three major prey items that may be captured and consumed at depth and, as such, remain undetected in prey remains

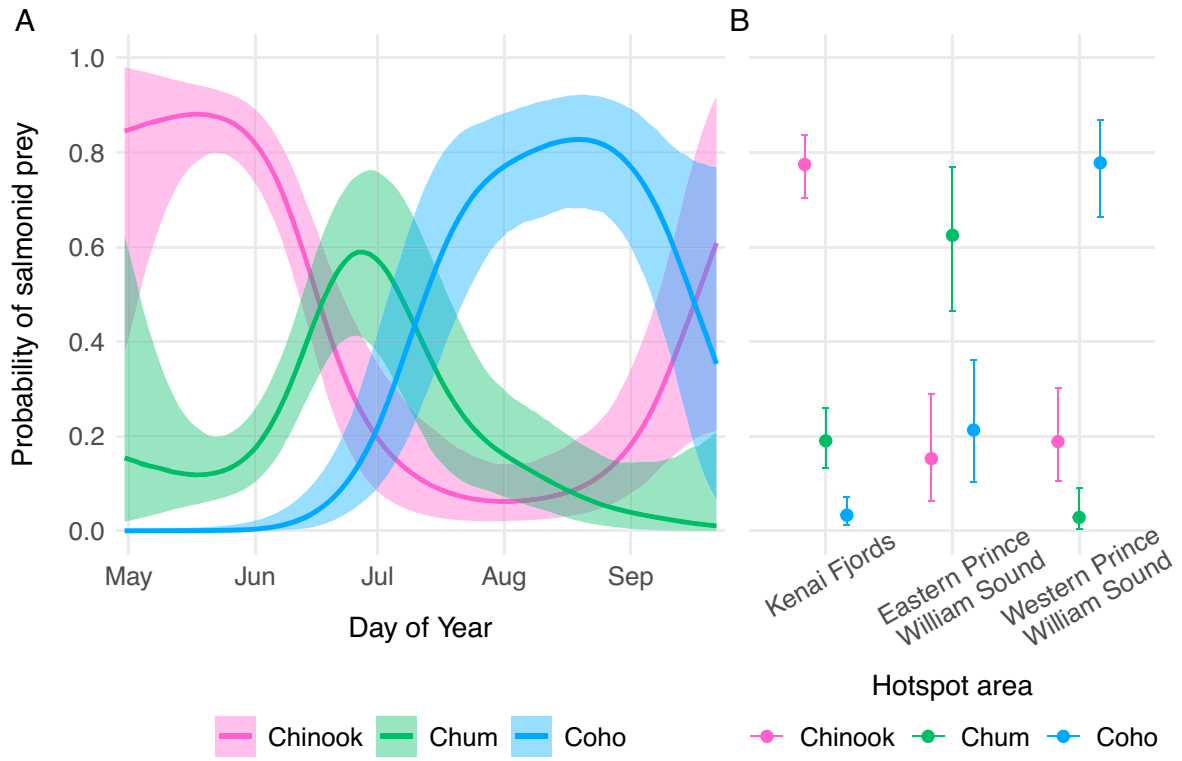

FIGURE 3 Conditional effects of prey remains models, which included either (A) a smooth function of day of year or (B) a categorical effect of foraging hotspot area (B). Ribbons (in A) and error bars (in B) indicate 95% credible intervals.

collected from surface waters: Pacific halibut, arrowtooth flounder, and sablefish (Table 3, Figure 4). As with prey samples, Chinook salmon was the predominant species in fecal samples from Kenai Fjords (71%) and chum salmon was the predominant species detected in eastern Prince William Sound (72%). In western Prince William Sound, diet samples were substantially more diverse, with the greatest contribution from Chinook salmon (35%). The main sampling periods largely aligned for both prey and fecal samples, though most fecal samples from western Prince William Sound were collected either before or after the main period in which prey samples were collected (Figure 4). Fecal samples were also collected in fewer years, and sample sizes were notably lower, especially from Prince William Sound (Tables 1 and 3).

Host DNA from 48 unique whales was identifiable in 82 samples. Pod identity was assigned for 68 samples based on photo identification at the time of sampling (Table 3). As with prey samples, fecal samples were collected from the AK2 pod across all three foraging hotspots, though there were differences in some of the other pods sampled across events.

Halibut was detected in all regions and made up >5% of at least one sample in May, June, July, and September. It was detected in the highest proportions in samples from the AE, AK, AD16, and AD8 pods but was also found in the diet of other pods. Arrowtooth flounder was detected in the greatest proportions in May, June, and September and in the highest proportions in samples from the AE and AI pods. In addition to the six major prey species, three fecal samples contained 1%–3% prowfish (*Zaprora silenus*), all of which were from Kenai Fjords.

For fecal samples, the multinomial model fit with hotspot area outperformed the model with day of year ($\Delta\text{ELPD} = -9.0$, $s = 4.5$) and again reinforced the statistical significance of the diet patterns we observed. Model results showed the strongest effects for chum and Chinook salmon (Figure 5, Table 4). The high proportion of chum salmon in eastern Prince William Sound (represented by the intercept) and the high proportion of Chinook salmon in Kenai Fjords were statistically significant (i.e., the 95% CIs did not include zero). Flatfish were more likely in western Prince William Sound, though not significantly so. Other species' proportions varied but effects were not consistently significant. Posterior predictive checks indicated sufficient model fit to the data (Appendix S1: Figure S4) and $\widehat{R}$ was 1.00 for all parameters. Including the random effect of pod did not meaningfully improve the model; ΔELPD (−4.4) was less than the magnitude of the SE (4.8).

TABLE 3 Fecal samples from six main fish prey species.

Area	Total samples	Sampling period (80%/all)	Main pods (*n*)	Major prey species	Proportion across all samples
Kenai Fjords	66	May 24–Jun 8/May 17–Sep 17	AD8 (22), AK (18), AD16 (9)	**Chinook**	**0.71**
				Chum	0.26
				Coho	0.00
				Halibut	0.03
				Arrowtooth	0.00
				Sablefish	0.00
Eastern Prince William Sound	12	Jun 15–Jun 30/May 9–Jul 1	AK (3), AE (2), AJ (1), AX48 (1)	Chinook	0.04
				Chum	**0.72**
				Coho	0.02
				Halibut	0.07
				Arrowtooth	0.13
				Sablefish	0.03
Western Prince William Sound	9	Jul 3–Sep 30/Jul 2–Sep 30	AE (4), AK (2), AB25 (1), AI (1), AJ (1)	**Chinook**	**0.35**
				Chum	0.20
				Coho	0.12
				Halibut	0.24
				Arrowtooth	0.09
				Sablefish	0.00

Note: The period within which 80% of fecal samples were collected and the range of dates within which all fecal samples were collected are shown for each area. The species with the highest overall proportion from each foraging hotspot is shown in bold. The main pods are those from which at least 10% of samples were collected, with the number of samples from that pod in parentheses. Pod was not identified in all sample collections.

Additional observations

The rich data available from fecal samples revealed several unique observations that complement the data generated from prey scales and tissue remains. First, fecal samples were collected from four individual whales across multiple foraging hotspots, all from the AK2 pod. Consistent with overall results, samples from these individuals included mostly Chinook salmon during the Kenai Fjords foraging hotspot and mostly chum salmon during the eastern Prince William Sound hotspot. Second, on May 29, 2018, fecal samples were collected from both adult female AD31 and her 4-year-old male offspring AD54 in the AD8 pod. Samples from both mother and offspring contained the same four species in very similar percentages: 81% and 77% chum salmon, respectively; 9% and 19% Chinook salmon, 9% and 4% Pacific halibut, and <1% each arrowtooth flounder. This unique collection event highlights an instance of high diet similarity between a known mother and dependent offspring—a pair of animals likely to share prey (Wright et al., 2016). Third, in 2018, we observed a change in foraging patterns, with killer whales foraging farther offshore than typical in Kenai Fjords. From fecal samples ($n = 14$) collected during this period, we documented a notably higher proportion of chum salmon (76%) that year.

Pod-specific diet and habitat use patterns

The primary pods we encountered differed across foraging hotspots (Figure 6). In Kenai Fjords, we documented the AD8 pod in 24% of encounters in which we collected a sample, followed by the AD16 (17%), AK2 (11%), AD5 (10%), and AK6 (9%) pods. In eastern Prince William Sound, we most often encountered the AJ (15%), AB (10%), AE (10%), AB25 (9%), and AK2 (8%) pods. In western Prince William Sound, we encountered the AE (19%), AB (11%), AI (11%), AK (10%), and AN (9%) pods most frequently.

This complicated our interpretation of pod-specific diet. However, several notable patterns emerged. First, the AE pod was the only pod for which we detected a majority of flatfish in fecal samples, including three of Pacific halibut and three of arrowtooth flounder. Second, the predominance of coho salmon in prey remains from western Prince William Sound was driven largely by

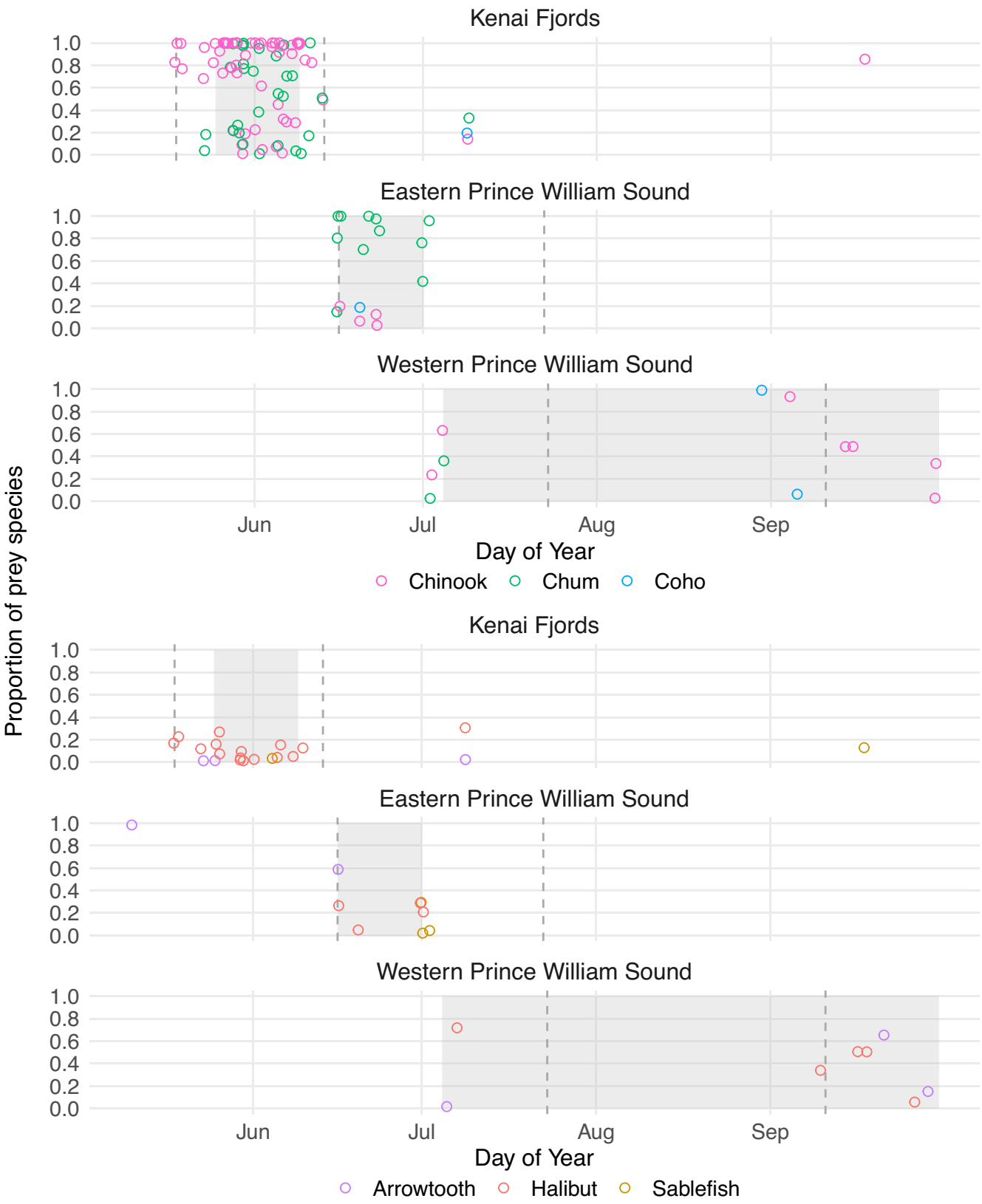

FIGURE 4 Proportions of prey species in fecal samples collected in each area from May through September. Salmonids are in the upper panels and groundfish are in the lower panels. Gray shaded periods indicate the days during which 80% of fecal samples were collected in each area. Each point represents the proportion of a unique sample made up by that prey species. Dashed lines indicate the periods in which 80% of prey samples were collected in each area, for comparison.

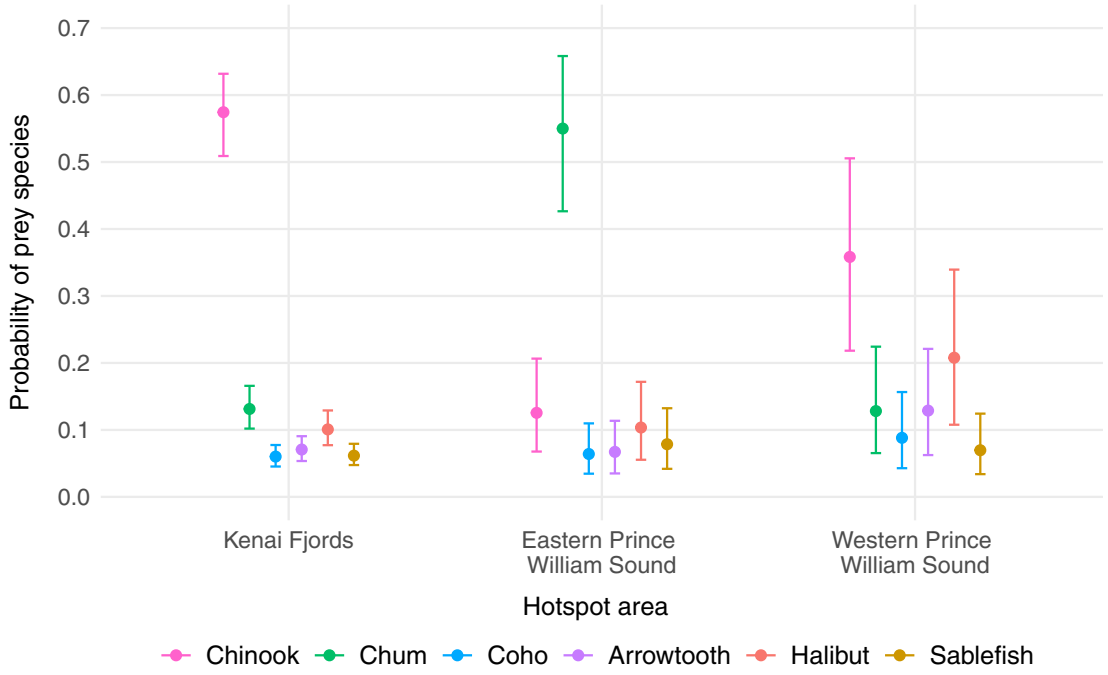

FIGURE 5 Conditional effects from the best fecal sample model with a categorical effect of foraging hotspot area. Error bars show 95% credible intervals for each prey species.

TABLE 4 Fecal sample model results for the probability of six main prey species as a function of foraging hotspot.

				95% CI	
Species	**Coefficient**	**Estimate**	**Estimated error**	**Lower**	**Upper**
Arrowtooth flounder	Intercept	−0.15	0.42	−1.00	0.65
	KF	0.29	0.45	−0.61	1.18
	WPWS	0.77	0.64	−0.52	2.01
Pacific halibut	Intercept	0.28	0.41	−0.55	1.09
	KF	0.21	0.45	−0.67	1.09
	WPWS	0.81	0.62	−0.41	2.02
Chum salmon	Intercept	**1.95**	**0.35**	**1.28**	**2.67**
	KF	**−1.20**	**0.38**	**−1.97**	**−0.46**
	WPWS	**−1.34**	**0.58**	**−2.49**	**−0.25**
Coho salmon	Intercept	−0.20	0.41	−1.02	0.61
	KF	0.17	0.44	−0.71	1.04
	WPWS	0.44	0.63	−0.80	1.67
Chinook salmon	Intercept	0.47	0.42	−0.34	1.31
	KF	**1.76**	**0.44**	**0.88**	**2.64**
	WPWS	1.17	0.60	−0.01	2.35

Note: Sablefish is the reference species and eastern Prince William Sound is the reference area against which intercepts and coefficients for Kenai Fjords (KF) and western Prince William Sound (WPWS) are compared. Statistically significant effects (those for which the 95% credible interval does not include zero) are shown in boldface.

samples from the AE ($n = 22$) and AB ($n = 7$) pods. Diet samples from other pods in western Prince William Sound showed a balance of Chinook ($n = 12$) and coho ($n = 11$) salmon. The predominance of Chinook salmon in Kenai Fjords and chum salmon in eastern Prince William Sound was more consistent among pods.

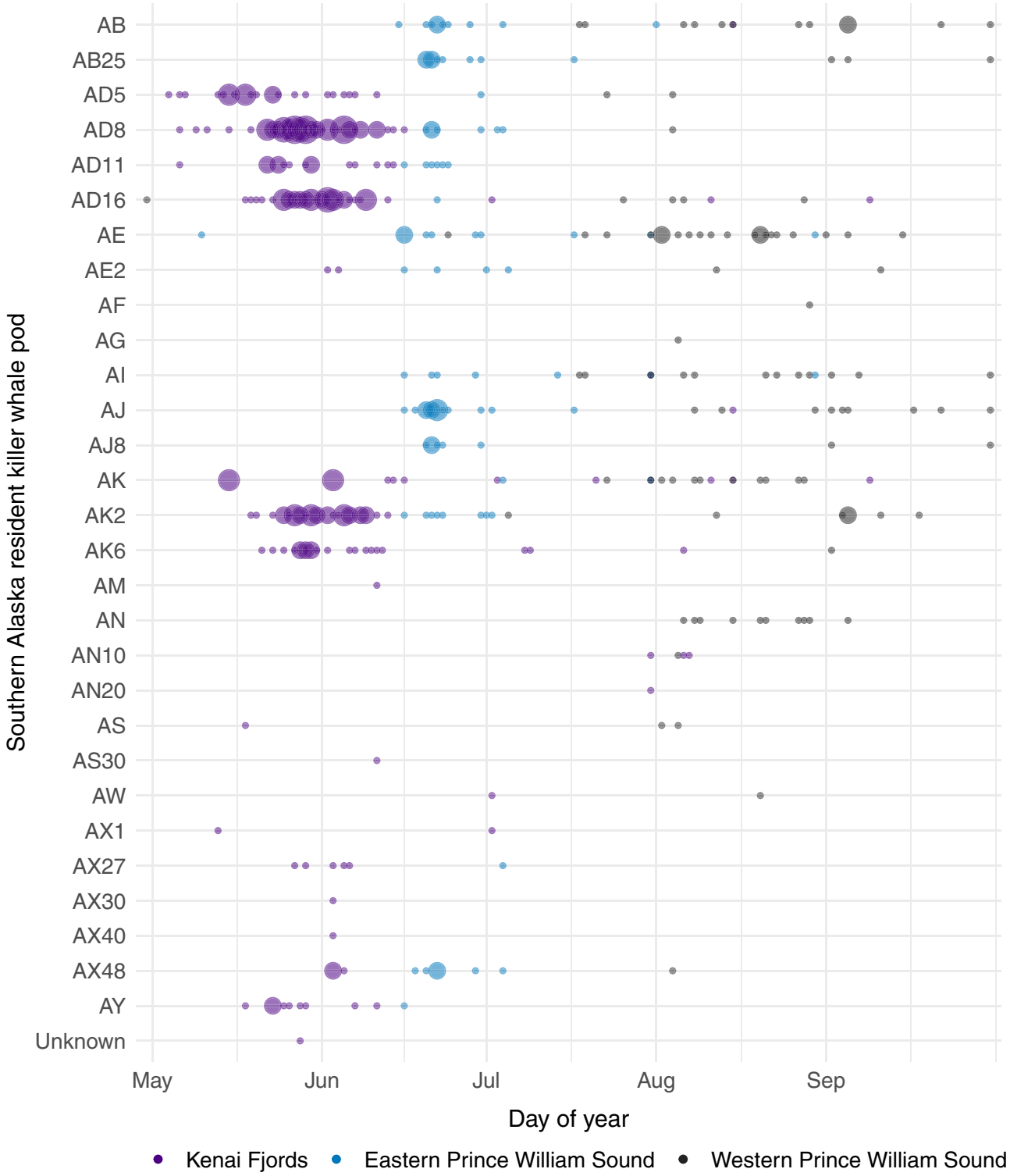

FIGURE 6 Pods documented during encounters in which we collected a prey remain or fecal sample, from May to September. Color indicates foraging hotspot area and point size indicates the number of unique encounters in which that pod was encountered for each day of the year. Over the course of this long-term study, some pods that were initially documented as a single pod were later split, either because their association patterns changed over time or because the initial groups in which they were documented did not represent consistent association. This includes the AD5 (later AD5, AD8, and AD11), AK (later documented as AK2 and AK6), AJ (later AJ and AJ8), and AN (later AN10 and AN20) pods.

In contrast, we collected diet samples from 11 different pods (AB, AD8, AD16, AE, AE2, AI, AK, AK2, AJ, AN10, and AX48) in more than one foraging hotspot (Appendix S1: Table S3). In general, samples collected from these pods in multiple foraging hotspots reflected the shift from one predominant prey to another, or from a predominant prey in one area to a more mixed diet in another. The AD8 and AK2 pods showed a clear switch from Chinook salmon in Kenai Fjords ($n = 56$, 82% of samples) to chum salmon in eastern Prince William Sound ($n = 10$, 91% of samples). The AK2 pod then switched back to Chinook salmon in western Prince William Sound ($n = 6$, 100%). However, sample sizes were small when examined by pod and hotspot.

DISCUSSION

In this study, we found that southern Alaska resident killer whales utilized different prey resources across spatiotemporally distinct foraging hotspots. The shift from primarily Chinook to chum to coho salmon across these hotspots likely reflects the relative availability of these three priority prey resources—as well as potential pod preferences. We also found that, even from May to September when salmon are abundant, southern Alaska resident killer whales supplement their diet with smaller proportions of other high-energy-content fishes—notably Pacific halibut, arrowtooth flounder, and sablefish.

The two sampling approaches generated broadly similar results in terms of primary species, timing, and pod identity. A notable exception is the prevalence of coho salmon in prey samples from the western Prince William Sound foraging hotspot (77%) relative to its proportion in fecal samples from that area (12%). The limited number of fecal samples from western Prince William Sound ($n = 9$) makes interpretation challenging; however, 73% of prey remains were collected from mid-July to late August (Figure 2), whereas all fecal samples were collected outside of that seasonal window (Figure 4). In addition, 80% of prey samples from western Prince William Sound were collected prior to 2008, while all fecal samples were collected after 2016, so changes in prey availability or diet preferences over time may also be relevant.

Pacific salmon are an abundant yet locally ephemeral resource in this region. Tracking the spatiotemporal variation in their phenology—including across species—extends foraging opportunities on this important prey resource for consumers. For example, the distribution of coastal brown bears (*Urus arctos*) and glaucous-winged gulls (*Larus glaucescens*) reflects the shifting distribution of spawning sockeye salmon (*Oncorhynchus nerka*) within a watershed (Schindler et al., 2013). Individual brown bears visit multiple salmon spawning sites in synchrony with their spawning phenology (Deacy et al., 2016)—and those that track spawning phenology for the longest consume the most salmon (Deacy et al., 2018). Though the pulsed nature of salmon availability in the marine environment is less well defined, the results of this study suggest that fish-eating killer whales may also capitalize on changes in Pacific salmon availability across relatively short spatial and temporal scales.

Populations with diverse diets may include specialized individuals or groups that feed on a restricted subset of prey (Bolnick et al., 2002). The prey patterns we documented may reflect killer whales tracking prey resources as well as different prey preferences among pods, which may be culturally transmitted (Filatova, 2024). The main pods detected in this study generally have different core use areas (Olsen et al., 2018) and represent multiple genetically unique maternal lineages (Barrett-Lennard, 2000; Barrett-Lennard & Ellis, 2001). There are two main maternal lineages in the southern Alaska resident killer whale population, each characterized by a fixed mitochondrial control region haplotype (Barrett-Lennard, 2000). The Kenai Fjords hotspot is dominated by one (which is more genetically similar to the southern resident population), while the eastern Prince William Sound hotspot is dominated by the other (which is more genetically similar to the northern resident population), and the pods commonly encountered in western Prince William Sound are more mixed. The AE pod exhibited the most distinct diet in this study—with six fecal samples consisting mostly of flatfish from May, June, July, and September in both regions of Prince William Sound, and a very high proportion of coho salmon prey samples in western Prince William Sound. The AE pod also has the most restricted range of the pods documented in our study area, with a core use area within the inside waters of Prince William Sound (Olsen et al., 2018). In contrast, samples from other pods, especially the AD8 and AK2 pods, for which sufficient sample size was available, matched the overall trend of high proportions of Chinook salmon during the Kenai Fjords hotspot and high chum salmon during the eastern Prince William Sound hotspot. On a finer scale, differences in foraging strategies among sex and reproductive classes have been documented in both southern and northern resident killer whales (Tennessen et al., 2023), and are worthy of further investigation in southern Alaska resident killer whales.

The shifts in diet documented for southern Alaska resident killer whales occurred within a limited season (May to September) and reflect the combined effects of spatial, temporal, and social factors. However, seasonal

changes in diet throughout the year are also common among top predators—even those with highly specialized foraging strategies. For example, wolves (*Canis lupus*) on Yellowstone National Park's northern range whose diets are dominated by elk (*Cervus elaphus*) hunt more mule deer (*Odocoileus hemionus*) and bison calves (*Bison bison*) in spring and summer (Metz et al., 2012). In Alaska, some wolves that hunt ungulates also eat large portions of Pacific salmon in summer (Stanek et al., 2017). Steller sea lions (*Eumetopias jubatus*) in the Aleutian Islands target seasonally abundant spawning and migratory hotspots of different fish prey (Sinclair & Zeppelin, 2002). As previously mentioned, southern resident killer whales eat almost exclusively Chinook salmon in spring and summer, but in fall and winter up to about half of their diet is made up of chum and coho salmon, steelhead (*Oncorhynchus mykiss*), lingcod (*Ophiodon elongatus*), big skate (*Rana binoculata*), and flatfishes (Hanson et al., 2021). In the North Atlantic, some killer whales prey switch between seasonally abundant Atlantic herring (*Clupea harengus*) and harbor seals (Vongraven & Bisther, 2014).

Lower quality or more difficult-to-access benthic prey (such as flatfish) may be important to killer whales if their phenological patterns mean that they are available when higher quality prey (such as Chinook salmon) are not (Abrahms et al., 2021). However, abundant but notably smaller and lower calorie fishes—especially pink salmon (*Oncorhynchus gorbuscha*) and herring—were not detected in proportions >1% in any fecal sample in this study. It is possible that the small proportion of prowfish found in fecal samples and the single herring prey sample we collected were secondary prey (i.e., a fish eaten by killer whale prey). Prowfish have been previously documented as prey of Pacific halibut but not salmon (Yang & Nelson, 2000; Graham et al., 2020); however, we detected prowfish in samples that were dominated by Chinook salmon (85%–98%) with little or no Pacific halibut (0%–13%).

In the northeast Pacific, fish-eating killer whale diet sampling has been highly biased to summer months and shallow coastal regions where salmon are likely to be abundant—including in this study (Ford & Ellis, 2006; Hanson et al., 2010; Saulitis et al., 2000). Weather, predictable seasonal ranging patterns of killer whales, and the relative ease of finding whales nearshore as opposed to in the open ocean contribute to this sampling bias. In this study, 59% of all prey samples and 76% of all fecal samples were collected in the foraging hotspot in Kenai Fjords, where protected waters and smaller killer whale group sizes created better conditions to search for samples. This hotspot was dominated by feeding on Chinook salmon. Accounting for spatiotemporal differences in sampling effort revealed the importance of other prey—especially chum and coho salmon—at other places and times, as has been found for other predators (Penteriani et al., 2005). Additionally, collecting fish scales or pieces of flesh when killer whales are observed feeding at the surface biases results toward salmonids, while species that are captured and consumed at depth (and those without scales) go undetected. A greater diversity of fish species has been detected through the analysis of resident killer whale fecal samples compared to prey species represented by surface sampling of prey remains (Ford et al., 2016; Hanson et al., 2021; Van Cise et al., 2024).

At present, southern Alaska resident killer whales' primary prey resources for more than half the year (October through April) remain unknown. Our current research effort likely misses other major foraging hotspots, even during the summer field season. The southern Alaska resident population is acoustically detected most often and with the largest estimated group sizes in late fall and winter in western Prince William Sound, and the peak in use of eastern Prince William Sound begins in early spring (Myers et al., 2021; Myers, 2023)—periods when no diet sampling took place. Previous satellite tagging also demonstrated high use of an area southeast of our study region near Kayak Island in many months of the year, implying yet another likely foraging hotspot, but weather and distance limit diet sampling opportunities (Olsen et al., 2018).

Knowledge of predator diets is frequently drawn from data collected over brief periods in specific regions, often focusing on unique subsets of a population that may not represent broader spatiotemporal scales. In the case of resident killer whales, extensive data collected from the southern resident killer whale population during summer months have been relied upon to describe the diet of resident killer whales generally (Adams et al., 2016; Chasco et al., 2017; Ohlberger et al., 2019). However, recent studies, including this one, indicate a greater degree of spatiotemporal, population-level, and socially driven variability in diet than had previously been observed (Ford et al., 2016; Filatova et al., 2023; Van Cise et al., 2024). This study adds a robust analysis to the growing body of diet research from other fish-eating killer whale populations in the North Pacific (Filatova et al., 2023; Van Cise et al., 2024; Volkova et al., 2019), illustrates a similar scale of spatiotemporal variability in this population to what is being described in other populations, and provides a high-resolution description of local diet and foraging patterns that can provide insight into the management of this population.

Finally, predator populations with highly specialized diets are likely to be more vulnerable to disturbance—including climate change impacts—than more generalist predators with greater flexibility in their diets (Wilson et al., 2008; De Gabriel Hernando et al., 2022). We found

that southern Alaska resident killer whales utilized three different primary salmonid prey resources across three main summer foraging hotspots, with substantial supplementation from other fishes. A relatively diverse diet may be important in supporting the large size of this top predator population, which is thought to be growing at a rate near maximum (Matkin et al., 2014). These findings have implications for the management of federally protected killer whales and their prey, some of which—especially Chinook salmon stocks—are currently listed or under consideration as endangered. This study adds to the growing body of work necessary to quantify how prey availability affects the southern Alaska resident killer whale population—as well as how killer whale predation may affect fish species that are important commercial, cultural, and subsistence resources.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Sequence data generated from fecal samples are available from the National Center for Biotechnology Information (NCBI) Genbank under BioProject PRJNA1068648. Data from prey remains and fecal samples and code used for statistical analyses (Myers, Olsen, Van Cise, et al., 2025) are available from Zenodo: https://doi.org/10.5281/zenodo.17647079.

ORCID

Hannah J. Myers https://orcid.org/0000-0002-2828-1874

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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