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Southern Resident Killer Whale Prey Selectivity in Relation to Chinook Salmon Stock and Size Composition within Canadian Critical Habitat

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Two populations of a fish-eating killer whale (*Orcinus orca*) ecotype occur in Canadian Pacific waters–northern and southern resident killer whales. The populations are listed as threatened and endangered, respectively, under the Canadian *Species at Risk Act*. Chinook salmon (*Oncorhynchus tschawytscha*) are a key prey item for both populations and declines in prey availability are a likely factor limiting resident killer whale recovery. Canadian southern resident killer whale (SRKW) critical habitat has been identified throughout the Salish Sea. The region is also habitat for a wide range of Chinook salmon populations with diverse life histories, physical characteristics, and trends in abundance. This report summarizes seasonal and spatial patterns in the relative abundance of 11 Chinook salmon stocks and four size classes throughout SRKW critical habitat in Canada, with a focus on summer months and areas from western Juan de Fuca Strait to the southern Gulf Islands. Chinook salmon stock and age composition data from SRKW prey remains (2007-2023) were evaluated, as well as model-based estimates of prey size composition. A second dataset of samples from recreational Chinook salmon fisheries, collected between 2014 and 2023, was used to parameterize geostatistical models that provided a prey field index. The two datasets were then compared to test for evidence of SRKW foraging selectivity. Finally, these results were evaluated in the context of hatchery enhancement in Canada, as well as differences among Chinook salmon stocks in biological characteristics and trends in terminal abundance.

Although all Chinook salmon stocks were observed in SRKW prey remains, Fraser River Spring 5_2 and Summer 4_1 stocks were most common. Independent of stock identity, relatively older Chinook salmon were more common in SRKW prey remains than younger individuals. Predictions from a season- and stock-specific size-at-age model indicated prey remains predominantly came from fish larger than 75 cm fork length. Depending on location and week, Columbia River Summer/Fall, Puget Sound, West Coast Vancouver Island (WCVI), and Fraser River Summer 4_1 Chinook salmon were among the most abundant stocks in fisheries-dependent samples. The two largest Chinook salmon size classes were most abundant in July and August and in locations near Port Renfrew. A simulation analysis comparing predictions from the fisheries-dependent geostatistical model to observed prey remains found mixed evidence of prey selectivity by SRKW. Fraser River Spring 5_2, Summer 5_2, and Summer 4_1 stocks occurred more frequently than expected in the prey remains while WCVI, Puget Sound, Columbia River Summer/Fall, and miscellaneous (i.e., "Other") stocks occurred less frequently than expected. The remaining stocks were present in prey approximately proportional to their abundance as predicted by the fisheries-dependent model. The two smallest Chinook salmon size classes ($55-65$ cm and $65-75$ cm fork length) were under-represented in SRKW prey remains, while the largest size classes ($65-75$ and $75-85$ cm) were over-represented. Canadian hatchery-origin salmon were identified in SRKW prey remains using PBT; however, these estimates are likely biased low due to incomplete PBT coverage during the sampling period. None of the stocks that showed evidence of positive selectivity are highly enhanced, while the Puget Sound and WCVI stocks, which are heavily enhanced, were negatively selected for. However, hatchery-origin fish may be important prey items in other locations or time periods. Terminal abundance, summed across all Chinook salmon stocks present in Canadian critical habitat, has not declined; however, stocks showed divergent trends in abundance. In particular, Fraser River Spring 4_2, Spring 5_2, and Summer 5_2 stocks have declined, while Fraser River Summer 4_1, East Coast Vancouver Island, and WCVI stocks have increased.

SRKWs rely on a diverse assemblage of Chinook salmon with the availability of stocks and size classes varying at fine scales, seasonally and spatially. However, large-bodied, energy-rich Chinook salmon are likely key prey, particularly during the spring and early summer when SRKW may be in relatively poor physical condition. Management interventions that increase the availability of large bodied or high lipid Chinook salmon during this period may be particularly important to recovering SRKW. Increases could occur by rebuilding currently depleted Chinook salmon stocks with these traits (e.g., Fraser Spring 5_2, Fraser Summer 5_2) or by increasing the mean individual size or lipid content of currently abundant stocks that overlap in space and time with SRKW foraging habitats.

1. INTRODUCTION

Canadian Pacific waters are home to three ecotypes of killer whales (*Orcinus orca*), each genetically distinct and exhibiting significant differences in morphology, behaviour, and diet. The resident fish-eating ecotype consists of two populations – the northern resident (NRKW) and southern resident killer whale (SRKW). Pacific salmon (*Oncorhynchus* spp.) form a large portion of their diet, with Chinook salmon (*O. tshawytscha*) identified as the dominant prey species (Ford and Ellis 2006, Ford et al. 1998, Hanson et al. 2010). From 1962 to 1973, both resident populations experienced significant removals as a result of the live capture fishery (Bigg and Wolman 1975). An annual census has occurred since the closure of the fishery, with recent data indicating that the NRKW population continues to exhibit a 2.5-3.5% annual increase and numbers approximately 341 individuals (DFO 2023*c*). The SRKW population has failed to maintain a positive growth trajectory and consists of only 74 individuals. The populations are listed under the *Species at Risk Act* as threatened and endangered, respectively (COSEWIC 2001, 2023).

The distribution of SRKW extends from central California to southeast Alaska (Thornton et al. 2022). During the summer months, SRKW historically made extensive use of the Salish Sea, which includes the Strait of Georgia, Haro Strait, Puget Sound, and Juan de Fuca Strait (Ford et al. 2017, Ford and Ellis 2006). More recently, areas west of Juan de Fuca Strait, including La Perouse Bank, Swiftsure Bank, and proximate submarine canyons have been identified as critical habitat during the summer as well as overwinter (Ford et al. 2017, Thornton et al. 2022). SRKW habitat use is associated with the migrations of Pacific salmon, and in particular Chinook salmon, which are found in the Salish Sea and associated continental shelf waters year-round (Chamberlin and Quinn 2014, Freshwater et al. 2021, O'Neill and West 2009).

One of several hypothesized drivers of low population growth rates in SRKW is reduced prey availability, with a particular emphasis on declines in Chinook salmon abundance. Observations of SRKW diets are typically dominated by Chinook salmon, though prey diversity increases overwinter to include coho salmon (*O. kisutch*), chum salmon (*O. keta*), and sablefish (*Anoplopoma fimbria*) (Ford et al. 2010*b*, 2016, Hanson et al. 2021). Additionally, SRKW demographic rates covaried with large-scale indices of Chinook salmon abundance (Ford et al. 2010*b*, Ward et al. 2009*a*), though these effects have proven difficult to estimate accurately given the long life span of killer whales (Vélez-Espino et al. 2015). Indices of Chinook salmon abundance were also correlated with changes in SRKW individual condition (Stewart et al. 2021), shifts in foraging behaviour (Holt et al. 2021), use of Salish Sea habitats (Ettinger et al. 2022, Stewart et al. 2023), and, via mass-balanced ecosystem models, caloric deficits in the SRKW population (Couture et al. 2022). Nevertheless, some evidence suggests relationships between SRKW demographic rates and Chinook abundance have weakened through time, perhaps due to competition with northern resident killer whales, which have increased in abundance (Nelson et al. 2024), or the increased effect of other anthropogenic impacts on individual health (e.g., mobilization of contaminants from lipid stores; physiological stressors such as physical and acoustic disturbance).

Evaluating SRKW prey needs, and tailoring management interventions to meet those needs, is challenging given the ecological diversity of Chinook salmon. Chinook salmon, like most Pacific salmon, are anadromous and semelparous, but differ from their congeners in several notable ways. Chinook salmon have the most extensive distribution of Pacific salmon in the eastern Pacific, extending from the Yukon River to central California. They exhibit diverse life history strategies during both freshwater (less than one to multiple years) and marine (less than one to more than five years) rearing. Due to their relatively old average age at maturity and

predominantly piscivorous marine diet, Chinook salmon reach the largest body size of Pacific salmon and can exceed 15 kilograms (Healey 1991).

Chinook salmon show strong spawning site fidelity and migration timing, resulting in many genetically distinct populations (Healey 1991, Quinn 2018). Chinook salmon populations may differ across several ecological dimensions including juvenile life history strategy (i.e., entering the ocean with (yearling) or without (subyearling) overwintering as juveniles in freshwater), adult freshwater migration phenology (i.e., spring-, summer-, or fall-run timing), and marine distribution. Unlike many species of Pacific salmon, a substantial number of Chinook salmon populations, predominantly fall-run subyearling individuals, spend their entire marine lives in coastal waters relatively close to their ocean entry locations (Chamberlin and Quinn 2014, Freshwater et al. 2021, O'Neill and West 2009). Other summer- and fall-run populations, as well as some yearling populations, migrate north considerable distances, but remain on the continental shelf (CTC 2022, Weitkamp 2010). Spring-run yearling populations that spawn in interior portions of large watersheds typically disperse offshore (CTC 2022, Weitkamp 2010).

Many Chinook salmon stocks (throughout used to refer to one or more distinct spawning populations) have declined in abundance over the past 50 years coincident with overfishing, habitat loss, and changes in productivity. Throughout California declines in freshwater habitat and changing environmental conditions have resulted in substantial reductions in life history diversity and less resilient fisheries (Munsch et al. 2022). Within the Columbia River watershed, five of seven evolutionarily significant units (ESUs) are listed as threatened or endangered under the Endangered Species Act (NMFS 2020). The Puget Sound Chinook salmon ESU also remains listed as threatened (Ford 2011). In southern British Columbia, the majority of assessed Chinook salmon Conservation Units (CUs) have been identified as threatened or endangered (COSEWIC 2018). Notably declines have occurred despite considerable investment in habitat remediation (Jaeger and Scheuerell 2023) and reductions in exploitation rates (CTC 2022). The broad spatial extent of declines, including in regions with relatively pristine freshwater habitats, has led to increasing scientific consensus that poor marine survival and reductions in age-at-maturity have reduced productivity and constrained recovery (Dorner et al. 2017, Freshwater et al. 2022, Ohlberger et al. 2018, Ruff et al. 2017, Welch et al. 2021).

Nevertheless declines in Chinook salmon abundance are not uniform. Declines in the abundance of spring-run yearling stocks in large watersheds have been particularly severe, but several subyearling summer-run stocks that spawn in the interior of the same watersheds have increased in abundance (Atlas et al. 2023, COSEWIC 2018, CTC 2022). Trends in the abundance of coastal fall-run stocks are mixed with some stocks, even within the same geographic region, increasing as others decline (Atlas et al. 2023, CTC 2022). As a result of these divergent patterns, Chinook salmon abundance may be relatively stable, increasing, or decreasing depending on which stocks are considered. For example, since subyearling summer- and fall-run stocks are abundant relative to spring-run stocks, especially given substantial hatchery production, the aggregate abundance of Chinook salmon in marine areas spanning southeast Alaska to Vancouver Island has remained relatively stable over the past 30 years (CTC 2022). Variability among Chinook salmon stocks in abundance trends, along with modest statistical power, may contribute to uncertain or weakening relationships between coarse estimates of Chinook salmon abundance and SRKW demographic rates (Nelson et al. 2024).

All else being equal, more abundant Chinook salmon stocks should be more prevalent components of SRKW diet. However, the contribution of different Chinook salmon stocks to the SRKW prey base may covary with ecological characteristics. First, Chinook salmon migration timing will

determine when specific salmon stocks are abundant in regions, such as the western portion of Juan de Fuca Strait, where SRKW disproportionately forage (Thornton et al. 2022). SRKW show seasonal patterns in condition, indicating they may experience prey limitations prior to observations in May (Fearnbach et al. 2020; J. Durban, pers. comm.). A general decrease in body condition over the winter months suggests that early run-timing (i.e., spring- and early summer-run) Chinook salmon stocks may provide a critical resource. Indeed, SRKW use of Salish Sea habitats has occurred later in the year coincident with declines in the abundance of Fraser River spring run Chinook salmon and increases in the abundance of stocks with later migration timing (Ettinger et al. 2022). Second, stock-specific marine distributions interact with run-timing to determine the extent to which specific Chinook salmon stocks overlap spatially and temporally with SRKW. While many Chinook salmon stocks are only present in southern British Columbia coastal areas immediately prior to spawning migrations, others are resident for their entire marine life history and are available as prey to SRKW year-round (Chamberlin and Quinn 2014, Freshwater et al. 2021, O'Neill and West 2009). Third, Chinook salmon stocks differ in age-at-maturity (Healey 1991, Ohlberger et al. 2018), size-at-age (Ohlberger et al. 2018, Xu et al. 2020), and lipid content (Freshwater and King 2024, Lerner and Hunt 2023, O'Neill et al. 2014), which collectively determine their relative energetic value. It is possible that SRKW select larger or more energy rich prey items disproportionately to their abundance. Indeed larger, older Chinook salmon individuals appear to be more common in resident killer whale diets than in proximate fisheries (Ford and Ellis 2006).

Determining the relative value of Chinook salmon stocks to SRKWs provides insight into the locations and times where SRKW may be most sensitive to reductions in prey availability. A subset of "high-value" Chinook salmon stocks may provide a stronger ecological signal linking SRKW demographic traits and individual condition to prey abundance. Evaluating the relative value of Chinook salmon stocks also allows resource managers to prioritize management interventions that are most likely to improve the availability of high-value stocks. While previous research has determined the relative contribution of Chinook salmon stocks to SRKW diets varies seasonally (Hanson et al. 2010, 2021), prey composition data have not been directly compared to the background prey field.

Here we use multiple lines of evidence to evaluate the relative contribution of different Chinook salmon stocks and size classes to SRKW diets in southern British Columbia. We note that due to data limitations our analysis focuses on Chinook salmon interactions from western Juan de Fuca Strait to the southern Strait of Georgia during summer months (May-October) and is not a comprehensive assessment of prey needs. Nevertheless, the region has been identified as critical habitat for SRKW (DFO 2017) and the condition of SRKW individuals is correlated with foraging opportunities in these areas (Ettinger et al. 2022, Stewart et al. 2021, 2023). First, we used samples from prey debris to evaluate the stock and size composition of SRKW foraging events in different portions of SRKW critical habitat. Second, we used samples collected from recreational fisheries as an index of the relative availability of different Chinook salmon stocks and size classes to SRKW. We used spatiotemporal models fit to fisheries-dependent data to predict stock composition and size composition at weekly intervals throughout SRKW critical habitat. Third, we conducted a simulation analysis to determine whether the observed prey samples deviated from model-derived predictions to test for evidence of SRKW selecting stocks or size classes disproportionately to their abundance. Fourth, we collated terminal abundance data (i.e., the abundance of mature Chinook salmon enumerated immediately prior to or after freshwater entry) to compare patterns in aggregate versus stock-specific abundance in Canadian critical habitat. Finally, we integrated these results with information on stock-specific differences

in Chinook salmon condition, hatchery contribution, age composition, and behaviour to identify potential management interventions to increase SRKW prey availability.

2. METHODS

2.1. STUDY AREA

Our analysis focused on data collected from Swiftsure Bank, west of Juan de Fuca Strait, eastward to the Gulf and San Juan islands in the southern Salish Sea (Figure 1). We constrained our analysis to this region based on the availability of SRKW diet data and previously published estimates of RKW habitat use (Thornton et al. 2022). Although SRKWs are found south to central California and north to central British Columbia, our study area comprises critical habitat that the population uses extensively from May through November (DFO 2017). Within the study domain we defined spatial strata to visualize SRKW diet and fisheries-dependent samples, as well as to generate spatially-explicit seasonal predictions (Figure 2); however, these strata were not incorporated as model parameters, which incorporated spatial data, i.e. coordinates, directly (additional details below).

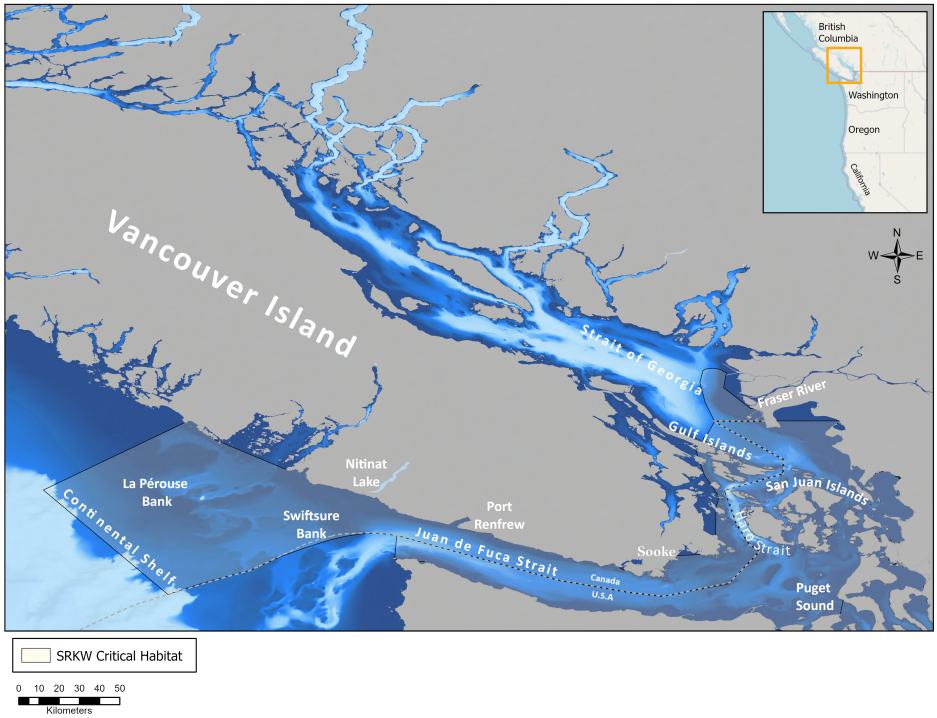

Figure 1. Study area in coastal southern British Columbia. Sea floor bathymetry represented by blue shading and SRKW critical habitat denoted by grey shaded polygon.

2.2. SRKW PREY REMAINS SAMPLING

Collection of resident killer whale prey remains began in 1974 as part of DFO's long-term study on the life history of killer whales. From 2003 to 2013 (designated as "early sampling period"), dedicated coastal surveys on RKW foraging were undertaken primarily using a 10 m power vessel (Ford et al. 2010*a*,*b*). Samples obtained from 2017 to 2023 are referred to as the "current

sampling period" and were collected primarily from surveys near Swiftsure Bank using 7 m rigid hull inflatable vessels (Thornton et al. 2022), with three years of survey effort (2018-2020) extending along Juan de Fuca Strait to Sooke (Figure 2).

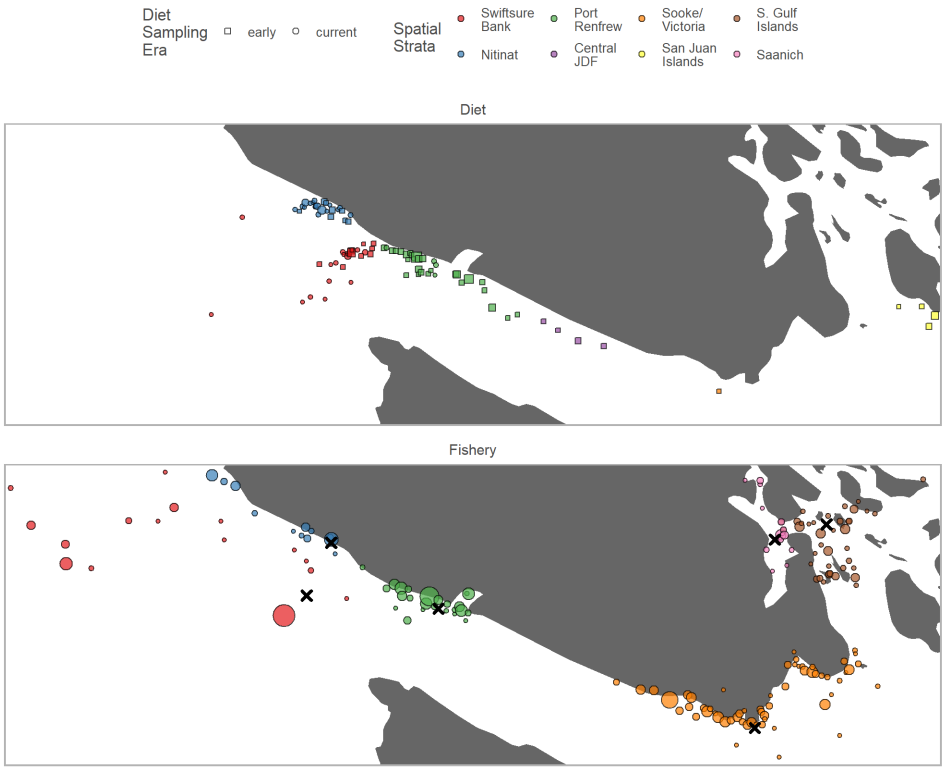

Figure 2. Locations of Chinook salmon stock composition samples originating from SRKW prey remains (top) and recreational fisheries (bottom). Squares and circles represent the early (2003-2014) and current (2017-2023) eras, respectively. Points are shaded by spatial strata and sized relative to the number of samples collected from that location over the entire study period. Black 'x' symbols in recreational fishery panel are representative locations within each strata that were used to generate spatial predictions with fitted models (Figures 14, 19). Central JDF refers to central Juan de Fuca Strait.

Sample collection protocols used in both the early and current sampling periods were similar. When whales were encountered, visual and photographic identification was initiated to establish ecotype, and if possible, determine the pod, matriline, and/or individual following identification techniques described in Bigg et al. (1987). Whale behaviour was observed for any sign of active foraging or feeding behaviour (predation events; see Stredulinsky et al. (2023) for a description of behavioural cues). When a predation event is suspected, the vessel was moved through the flukeprint of the whale to look for floating scales and tissue. Biological samples (e.g., scales, prey tissue) were collected using a dip net and removed from the net using sterile forceps and placed into 20 mL glass scintillation vials containing 10 mL of 95% ethanol for subsequent identification. All three SRKW pods utilize the western portion of Canadian critical habitat during summer and prey remains were collected from each pod, though too few were available to test for pod-specific differences.

It is possible that sampled prey remains may not be representative of SRKW diets. First, species diversity in SRKW diets estimated from fecal samples (presumed to be unbiased) is typically higher than that from prey debris samples (Hanson et al. 2021), likely due to species-specific differences in the likelihood that debris is collected. These effects are not relevant here, however, because we focused on only Chinook salmon. Second, prey remains may reflect prey consumed near the surface, which may be more likely to be surface-oriented or large-bodied prey. Yet tagging data suggests that resident killer whales identify Pacific salmon prey at moderate depths, pursue individual prey to deep water, and then consume prey near the surface (Wright et al. 2021). These behaviours are consistent across a relatively broad range of Pacific salmon species and size classes (Wright et al. 2021). Third, SRKW sampling events may not be independent. Without a statistical model we cannot quantify spatial or temporal autocorrelation in prey remains; however, samples collected on the same day and in close proximity often originated from multiple stocks, suggesting modest autocorrelation (Figures A.1, A.2).

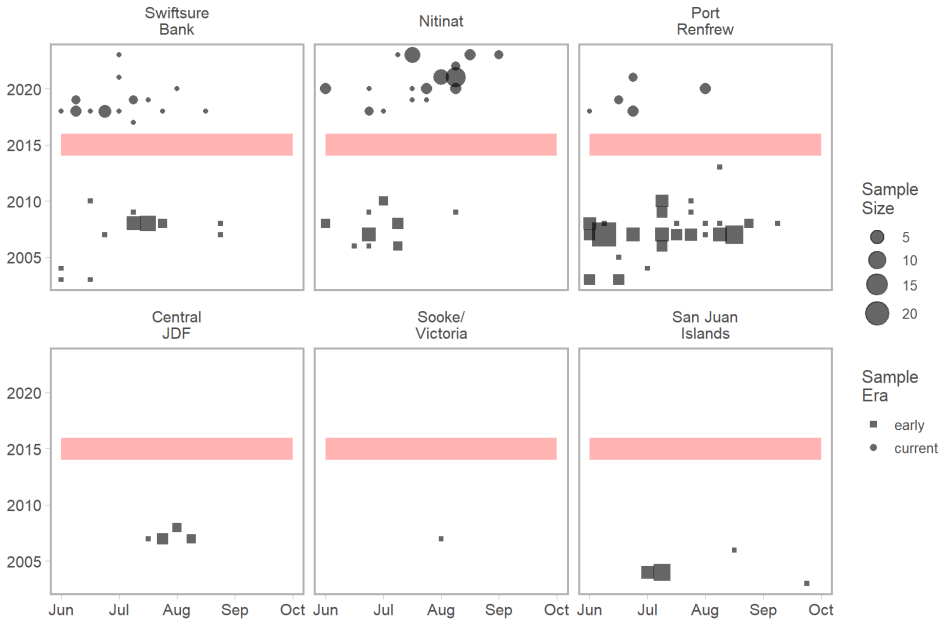

Figure 3. Temporal distribution of Chinook salmon stock composition samples from SRKW prey remains. Strata (panels) correspond to spatial domains in Figure 2. Early and current sampling periods are represented by squares and circles, respectively, with red polygon showing intervening years. Point size scaled to number of samples collected within a given week and year.

2.3. RECREATIONAL CHINOOK SALMON FISHERIES SAMPLING

DFO's South Coast Area Stock Assessment section collects biological data from recreational saltwater fisheries throughout southern British Columbia. Since 2014, these data have included scale and tissue samples, fork length measurements, information on whether a fish's adipose fin is intact or clipped, and, when present, coded wire tags (CWT) that assign an individual to a specific hatchery release group. Additional details on how biological samples are used to determine age and stock identity are provided below.

Fishery samples were collected from three field programs. The majority originated from the dockside creel observer program, where samples are collected during interviews with recreational fishers. The dockside observer program only samples landed catch (i.e., fish retained for harvest).

A portion of samples were collected by a citizen science program, the Avid Anglers, which is a collaboration between DFO, the British Columbia Sport Fishing Institute, recreational harvesters, and sport fishing guides. Participants provide data on size and adipose clip status for all the salmon that they encounter (kept and released), as well as samples for genetic stock identification (GSI). The samples are predominantly from landed catch; however, the Avid Anglers also collect genetic samples from fish released from non-retention fisheries (though the frequency of sampling in non-retention fisheries varies spatially). Finally, samples from 2022 and 2023 include data collected by DFO Science staff during Reference Fisheries, a research program in collaboration with the Sport Fishing Institute to collect biological data to evaluate the impacts of mark selective fisheries. Reference Fisheries sample all encountered Chinook salmon and are therefore representative of both landed and released catch. We did not stratify based on field program because Avid Angler samples from landed catch could not be reliably distinguished from dockside sampling of landed catch.

Fisheries-dependent data may be biased due to factors such as gear selectivity or fisher behaviour. These effects are magnified by management interventions such as mark selective fisheries or size limits. Recreational fisheries in the study area have been impacted by management interventions that vary seasonally, spatially, and among years (Figure A.3; see Dobson et al. 2020 and DFO 2023 for details). While our dataset includes samples from released individuals, which are presumably less biased than landed catch, these made up a relatively small proportion of the total (approximately 5%). A preliminary analysis indicated stock composition estimates were similar regardless of whether samples from released fish were or were not included (results not shown), and all subsequent analyses included released samples. Unfortunately a more robust evaluation of selectivity effects was not possible due to the unbalanced timing and location of management measures; however, we qualitatively describe the potential impacts of management measures to our conclusions in the discussion.

Biological samples included a location code representing the fishing location (either reported to the creel observer or recorded by the Avid Angler or science staff). Location codes were georeferenced to provide a latitude and longitude for each sample. In other words, each fishery sample had an approximate location representing a commonly used fishing site, not a precise location based on where the fish was captured (Figure 2). Although coverage varied spatially, sampling occurred in some regions in all months (Figure 4).

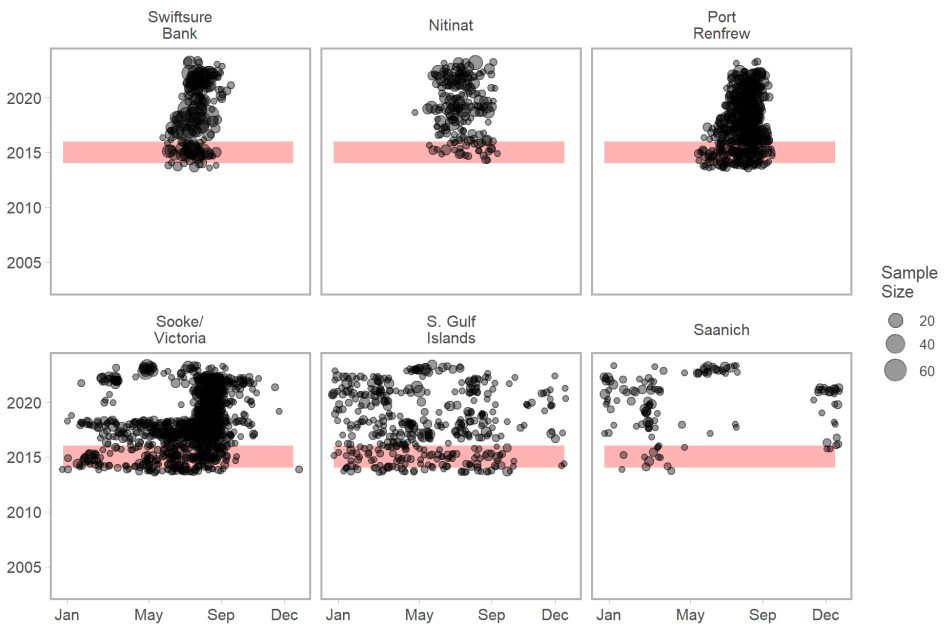

Figure 4. Temporal distribution of Chinook salmon stock composition samples from recreational fisheries. Strata (panels) correspond to spatial domains in Figure 2. The intervening years with no prey samples is represented by a red polygon showing that no fishery samples are available from the early SRKW prey remains sampling period (Figure 3). Point size scaled to number of individual samples collected within a given fishing location, week, and year. Points have been jittered to maximize visibility. Note that fishery samples, unlike prey remains samples, were collected throughout the year.

The primary advantage of this dataset relative to more commonly used CWT recovery data is the precision with which samples can be assigned to a location and time period. The CWT program aims to estimate stock-specific exploitation rates across a broad spatial scale—a similar, but distinct, goal to estimating spatially and temporally explicit estimates of stock composition. Because CWT-derived estimates of exploitation rates require a relatively large number of tag recoveries per fishery to be sufficiently precise, they are commonly aggregated at seasonal (e.g., multiple months) and regional scales (e.g., southwest Vancouver Island vs. southern Strait of Georgia). Furthermore, several Canadian stocks, including Fraser River Spring 5_2 and Summer 5_2, that may be key prey of SRKWs are not adequately represented by current CWT indicators.

2.4. ASSIGNING SAMPLES TO STOCKS, SIZE CLASSES, AND HATCHERIES

2.4.1. SRKW Prey Samples

Scales collected after an SRKW predation event were mounted and visually examined using Leitz Neopromar projectors to evaluate marine and freshwater annuli patterns. Species and age were determined from scale readings by experienced agers at the Fish Ageing Laboratory at the Pacific Biological Station's Sclerochronology Lab (Fisheries and Oceans Canada, Nanaimo, British Columbia, Canada). The laboratory provides an estimate of the number of years a salmon spent in both freshwater and ocean habitats (i.e., freshwater and marine age respectively) based on annual growth increments. Since the majority of Chinook salmon growth occurs during ocean residence and freshwater ages were not always available for fishery samples, we focused analyses on marine age. Additionally, we incorporated aging error in estimates of SRKW prey remains and

used marine age, including this error, to predict the fork length of SRKW prey based on stock-specific size-at-age relationships (details in Appendix B).

Scale samples and post-predation tissue remains were submitted to DFO's Molecular Genetics Laboratory at the Pacific Biological Station for species and stock identification. Chinook salmon stock identification followed the methodology described in Beacham et al. (2018). Briefly, DNA was extracted and PCR amplification of 321 target amplicons was conducted using a primer pool developed from published Chinook salmon sequence data. Samples were then identified to stock using either a) a targeted SNP amplicon sequencing methodology or b) parentage based tags (PBT). Under the PBT program hatchery broodstock are genotyped, allowing sampled offspring to be assigned to parent individuals and identified as hatchery origin (details below), with a high degree of confidence (Beacham et al. 2022). We aggregated individual stock assignments to improve interpretability (additional details below).

2.4.2. Recreational Fishery Samples

Stock identity for samples collected from the recreational fishery was inferred by matching recovered CWTs or otoliths to release cohorts or using tissue samples with SNPs or microsatellites (Beacham et al. 2006, 2022). Given the large number of Chinook salmon stocks present in southern British Columbia, we aggregated individual assignments, which were made at approximately the scale of spawning populations, to make subsequent analyses tractable.

In Canada, Chinook salmon are assessed at the CU level (Holtby and Ciruna 2007); however, domestic management actions often focus on stock management units (SMUs) that contain one or more CUs. While CUs within an SMU may not spawn in close proximity, a single SMU typically has a relatively homogeneous marine distribution and migration phenology. CUs by definition exclude hatchery-origin fish, while SMUs do not. Since our analysis was focused on the Canadian management context, we aggregated most Canadian populations at the SMU level (Figure 5, Table S1). We further aggregated Lower Georgia Strait, Middle Georgia Strait, Upper Georgia Strait, and Southern Mainland Inlet SMUs as East Coast Vancouver Island and Southern Mainland Inlets (ECVI/SOMN) since these SMUs were relatively rarely encountered (Figure 5, Table S1). We assigned the remaining individuals to one of four regional groupings: Puget Sound, Columbia River and Snake River spring-run, Columbia and Snake river summer/fall-run (including Willamette River spring-run fish due to a similar marine distribution), and an aggregate ('Other') including rare northern British Columbia, Washington and Oregon coastal, and California populations (Figure 5, Table S1). We emphasize that the Columbia River and 'Other' stocks pool populations with disparate life histories, but given the Canadian management focus of this analysis and the necessity to fit a tractable model, our groupings allow for reasonable inference to be drawn. Throughout this manuscript we use the terms "stock" and "stock composition" when referring to these specific groupings, as well as generic aggregates of Chinook salmon populations.

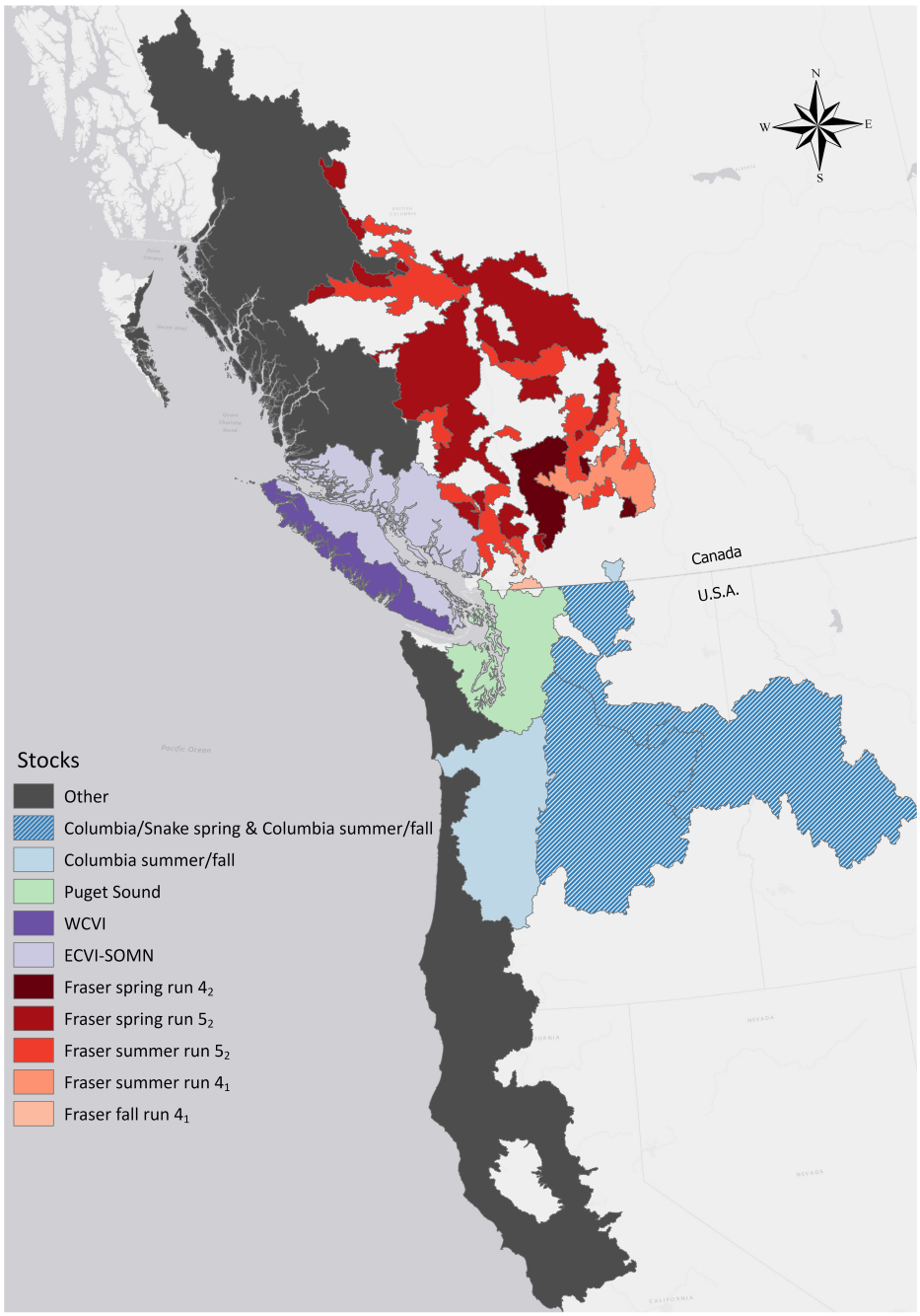

Figure 5. Watersheds containing natal streams for each Chinook salmon stock. Note that all watersheds with Columbia River Spring populations also contained Columbia River Summer/Fall populations and are represented by hatching.

To model variability in Chinook salmon size we created four size bins based on fork length at capture: less than 65 cm, 65-75 cm, 75-85 cm, and greater than 85 cm. Fish smaller than minimum size limits (either 62 or 45 cm fork length depending on management area) may be sampled and released; however, we included only fish larger than 55 cm in subsequent analyses. Age data

for a subset of individuals (n = 7815) were available from CWTs, PBTs, or estimated using scale annuli (details above).

We used multiple approaches to identify the relative contribution of hatchery-origin fish in samples from recreational fisheries. Fish with missing adipose fins were identified as hatchery-origin. Mark rates (the proportion of hatchery releases where adipose fins are removed) are nearly 100% in Washington and Oregon hatcheries (Anderson et al. 2020, ODFW 2022, WDFW 2021), but British Columbia hatcheries only mark a relatively small proportion of individuals (PSC 2016). Therefore we also used otolith thermal marks and genetic sampling to identify hatchery-origin individuals.

British Columbia hatcheries began implementing PBT in the 2013 brood year and while coverage at large enhancement facilities is typically high, it has varied through time (Figure A.4). Individuals with a PBT assignment were identified as hatchery-origin, while those identified as originating from stocks that are not present in the PBT baseline were identified as wild. Finally, individuals with intact adipose fins and GSI assignments to stocks with low mark rates and no PBT data (e.g., California, Alaska) or belonging to brood years in which the relevant British Columbia hatchery had a relatively low PBT rate (here defined as less than 80% broodstock coverage (Figure A.4)) were assigned an "unknown" classification. Given that many recreational fishery samples could not be definitively assigned hatchery or wild status, and that hatchery contributions covary with stock identity, we did not fit a statistical model to hatchery assigned data.

Unlike previous analyses (e.g., Freshwater et al. 2021), we did not scale estimates of stock composition by Chinook salmon catch per unit effort to derive an index of stock-specific abundance because the primary comparison of interest was between the composition of the fishery and the composition of prey remains. Furthermore, estimates of catch and effort are typically most reliable at creel subarea and monthly scales (or coarser), which would dilute the spatiotemporal resolution of stock composition estimates. Finally, we are already assuming the recreational fishery samples Chinook salmon composition in a manner analogous to SRKWs (explored in detail in Discussion). Estimates of stock-specific abundance incorporate additional selectivity assumptions that may not be valid.

2.5. PROPORTION HATCHERY-ORIGIN SPAWNERS

To better understand variation among Canadian stocks in hatchery enhancement, we present both individual-based estimates of hatchery contributions (described in the previous section) and estimates of the proportion hatchery-origin spawners (pHOS). Estimates of pHOS were provided by Fisheries and Oceans Canada's Salmonid Enhancement Program and were available for return years between 2014 and 2022, though the number of years available varied among spawning populations. Since each stock contains multiple spawning populations, we calculated mean pHOS, by stock, using a hierarchical model with random intercepts for population and a beta link. Estimates of mean pHOS at the stock level should be interpreted with caution since relatively few populations per stock were considered and the means are not weighted by the relative abundance of each population. Additionally, pHOS does not provide an index of the *overall* abundance of hatchery fish within a stock, only an index of hatchery abundance on the spawning grounds.

2.6. CHINOOK SALMON TERMINAL ABUNDANCE

Recent trends in Chinook salmon abundance have been reported elsewhere (e.g., Atlas et al. 2023, CTC 2024); however, for additional context we present terminal abundance estimates

grouped by the focal stocks in our analysis. Terminal abundance estimates include escapement as well as harvest in terminal areas, with the exception of ECVI/SOMN estimates which include only escapement. Terminal areas are generally defined as freshwater, but some stocks' estimates also include harvest in marine fisheries proximate to freshwater (Table C.1). We present terminal abundance data from 1982 to 2023, but four-year means were used to interpolate 2023 values for most Washington Coastal (grouped with Other throughout this manuscript) and Puget Sound stocks. Additional details in Appendix C.

Terminal abundance estimates provide an index of abundance in Canadian SRKW critical habitat, but will be biased relative to true abundance because they exclude harvest in marine fisheries and natural mortality. Additionally, terminal abundance estimates fail to account for stock-specific differences in run timing, migration routes, and, in the case of resident Chinook salmon stocks, immature individuals that rear in SRKW critical habitat for extended periods. These factors will impact prey abundance available to SRKW; however, accounting for their effects was outside the scope of the current analysis (additional details described in Discussion).

2.7. STATISTICAL MODELS

2.7.1. Stock Composition

Stock composition data represent the proportion of a total sample belonging to each stock. Since, when a CWT is not present, stock identity is estimated based on molecular markers and mixture models, inference based on stock composition data should account for at least two sources of uncertainty—the variability associated with the sample size of an observation and the variability associated with the precision of the stock assignment. Summary statistics, such as the mean relative abundance of a stock, often fail to account for differences in sample size among sampling events, as well as autocorrelation among sampling events. For example, stock composition data collected in adjacent spatial strata are unlikely to be statistically independent. Similarly, uncertainty in genetic stock assignment probabilities is often ignored by using arbitrary thresholds (e.g., 75% probability) to assign an individual to a stock with absolute confidence.

To address these issues, we used statistical models to evaluate differences in the relative abundance of stocks among locations and months, account for variation in sampling intensity, and propagate uncertainty associated with individual stock assignments. Dirichlet multinomial generalized linear models (GLMs) and generalized additive models (GAMs) are increasingly used to draw inference on proportion data arising from continuous measurements (Douma and Weedon 2019), such as individual stock assignment probabilities (Freshwater et al. 2021, Jensen et al. 2022). However, the Dirichlet multinomial distribution cannot readily account for zero observations (Douma and Weedon 2019, Jensen et al. 2022), which are common in composition data with relatively small sampling events and rare groups, and the underlying parameters are difficult to interpret. Additionally, there are currently no spatially explicit Dirichlet multinomial GLMs or GAMs. As an alternative, we used multivariate Tweedie GAMs to quantify variability in stock composition through time and space. Briefly, the multivariate Tweedie assumes composition data arise from a thinned and marked Poisson process that can be expressed as a Tweedie distribution (Foster and Bravington 2013, Thorson et al. 2022). Simulation studies suggest the multivariate Tweedie has similar or superior performance to the Dirichlet multinomial when analyzing composition data (Thorson et al. 2023).

We attempted to fit various model structures to the SRKW prey remains data, but there were too few observations to adequately capture variability among seasons, spatial strata, and the

early and current sampling periods. Thus we only qualitatively assess patterns in stock and size composition for these data.

We fit multivariate Tweedie GAMs to Chinook salmon fisheries-dependent data to quantify seasonal and spatial variability in stock composition, while accounting for interannual variability in abundance. We defined a sampling event j, representing all individual fish sampled for stock identity in a given fishing location, week, and year. Since assignment probabilities were identified at the scale of spawning populations (i.e., sub-stock), we aggregated GSI data into stocks (Table S1), by summing, within j, all probabilities associated with populations belonging to stock s. Thus the observed density of s within a sampling event d_{j_s} could take any continuous positive value between zero (all sampled individuals had a zero probability of being assigned to s) to the total size of the sample n_j (all individuals were assigned to s with 100% probability). Since individuals often had non-zero probability of belonging to multiple stocks, d_{j_s} was often not an integer. When stock identity was inferred from a CWT, PBT, or otolith thermal mark then the assignment probability for that individual was one. Since d was a function of n_j the precision of mean composition estimates scaled with the number of individuals included in a sampling event.

We estimated changes in the relative abundance of each Chinook salmon stock using a Tweedie distribution with mean μ, power p, scale ϕ, and a log link:

$$d_{j_s} \sim \text{Tweedie}\left(\mu_{j_s}, p, \phi\right), \tag{1}$$

$$\log(\mu_{j_s}) = \alpha_s + \alpha_{y_s} + f_{w_s} w + f_{g_s,h_s}(g,h) \tag{2}$$

Where α_s is an intercept representing the mean abundance of each stock, α_{y_s} is a random intercept representing year-specific y changes in the abundance of stock s, f_{w_s} is a Gaussian process smooth function for sampling week w that varies among stocks, and f_{g_s,h_s} is a Duchon-spline smooth function for sample location (easting g and northing h) that varies among stocks. We modeled α_{y_s} assuming a hyperdistribution with mean zero and standard deviation σ_y. The smooth functions accounted for seasonal variation in stock composition, while the Duchon-spline smooth functions estimated spatial variation in the relative abundance of different stocks (Thorson et al. 2022). We constrained the model to a maximum of 20 and 35 basis dimensions for the sampling week and location smooths, which allowed for a relatively high degree of non-linearity (for context two basis dimensions approximate a quadratic function), while ensuring model convergence.

Predictions from a multivariate Tweedie model reflect continuous estimates of the mean density of an observation (here a given stock) in a sample, as well as its standard error. Both means and standard errors are then rescaled as estimates of composition bound by 0 and 1 (Thorson et al. 2022, 2023). We used the fitted model to generate predictions of marginal effects representing a) mean seasonal, b) mean spatial, c) spatially-explicit seasonal, and d) spatially-explicit annual predictions of stock composition in the Chinook salmon fishery. These predictions were used to qualitatively assess patterns in stock-specific abundance. We restricted seasonal predictions to between May and October (May to September for western strata) because sampling was spatially unbalanced outside that period, which may result in unreliable model predictions.

In the case of mean spatial effects, we present spatial predictions scaled by a stock's maximum predicted abundance. Scaled predictions can be interpreted as representing spatial variation in abundance *within* a stock, while unscaled spatial predictions represent spatial variation in stock composition. Mean spatial predictions are projected onto a grid, representing a smooth

surface of variability in stock composition. Conversely, spatially-explicit seasonal and annual predictions are generated for specific point locations, not a grid, to make visualization possible. We generated predictions for a single location near the center of each strata (X symbols in Figure 2). We note that these points were chosen arbitrarily and if they were shifted the predictions would change.

To evaluate model fit we calculated randomized quantile residuals with fixed-effects at their maximum likelihood estimates and random effects sampled with Markov chain Monte Carlo (MCMC) (*sensu* Rufener et al. 2021). We used these simulated values to compare model predicted stock composition to observed stock composition and ensure the model was generating plausible predictions, i.e. posterior predictive check. We fit models using the mgcv package (Wood 2011), generated predictions using the mvtweedie package (Thorson et al. 2022, 2023), and generated MCMC residuals using the sdmTMB package (Anderson et al. 2022). All analyses were conducted in R version 4.4.0 (R Core Team 2021) and relevant data and model code are available on zenodo.

2.7.2. Selectivity Analysis

We used the fitted model to parameterize a Monte Carlo simulation to test for evidence of SRKW diet selectivity. Specifically, we tested whether the observed stock composition of SRKW prey remains differed from the predicted stock composition, as indexed by the fishery, while accounting for the relatively small number of prey remains collected. Since concurrent fishery samples were not collected during the early prey sampling period this analysis was restricted to prey remains collected during the current period, which were all collected in locations west of central Juan de Fuca Strait (Figure 2).

The fishery-dependent model was used to predict a vector of mean stock composition, $\hat{\boldsymbol{\pi}}$, of length S (where S is the number of stocks) for each SRKW prey sampling event based on the location, week, and year in which the prey sample was collected. Since SRKW sampling events rarely collected more than one sample from a given location, we pooled samples collected from the same strata, week, and year, using the mean latitude and longitude of the original samples, to create a new sampling event j' for the selectivity analysis. We accounted for model uncertainty by assuming the proportional contribution of each stock came from a random normal distribution with mean $\hat{\pi_s}$ and standard deviation σ_{π_s}, which were rescaled to ensure the composition estimate was bound by 0 and 1. We then used the observed stock composition at j' based on prey remains sampling π and $\hat{\pi}$ as the mean proportions in random draws from a multinomial distribution. We drew n_{sim} samples where n_{sim} is equal to the number of samples collected in an SRKW sampling event $n_{j'}$, resulting in two vectors $\boldsymbol{Y_{obs_{j'}}}$ and $\hat{\boldsymbol{Y_{sim_{j'}}}}$, representing individual counts of each stock at each event. We summed across all sampling events to calculate the total number of individuals in each stock across all events, $\boldsymbol{Y_{obs}}$ and $\hat{\boldsymbol{Y_{sim}}}$. Finally, we converted both vectors to proportions and calculated the difference $\boldsymbol{\Delta Y}$.

The simulation analysis explicitly accounts for seasonal, spatial, and interannual variability in stock composition, while propagating uncertainty due to genetic stock assignment, estimated parameters within the fishery model, and the sample sizes of the prey remains themselves. We repeated the simulation analysis 500 times to account for variability in each dimension of uncertainty. We used the distribution, among simulations, of $\boldsymbol{\Delta Y}$ to visualize selectivity with positive (negative) values representing a stock occurring more (less) commonly in the observed than the predicted stock composition.

2.7.3. Size Composition

We fit a similar model to quantify variation in size composition of Chinook salmon captured by the recreational fishery. The model was equivalent to Equation 1, but instead of sample j representing individuals belonging to stock s, it represented individuals belonging to size class c. Since individual recreational fishery samples were measured, and therefore could be assigned to a size bin with zero error, we assumed that the contribution of each class followed a negative binomial ('NB1', Hilbe 2011) distribution modeled with a log link. As with the stock composition model, mean predictions and their standard errors were scaled to proportional estimates post-hoc, which were used to visualize marginal effects and conduct a simulation exercise testing for evidence of selectivity. The size selectivity analysis propagated uncertainty associated with the estimated size of prey remains due to aging error and variability in stock-specific size-at-age relationships (this is broadly analogous to stock assignment uncertainty in the previous section; (details in Appendix B)). We evaluated model performance using previously described diagnostics.

2.8. SENSITIVITY ANALYSIS

We conducted two sensitivity analyses. The first aimed to account for deviations between the stock composition of the recreational fishery and SRKW prey remains due to size-selective predation by SRKWs. We excluded samples from the recreational fishery smaller than 75 cm fork length (>70% of prey remains estimated to be greater than this size) and refit the model (Equation 1). In the second, we accounted for prey remains samples that were collected during times and locations when fisheries were closed or impacted by size limits (Figure A.3). We excluded the small number of impacted samples (11 of the stock samples and eight of the size samples) and repeated the selectivity analysis. Additional details on methods and results are reported in Appendix D.

3. RESULTS

3.1. SRKW PREY REMAINS

151 samples from prey remains were collected between 2003 and 2013 (the early sampling period) and 85 samples were collected between 2017 and 2023 (the current sampling period). The number of samples varied among spatial strata and month (Figure 6). During the early period the majority of samples were collected from Swiftsure Bank, Nitinat, and Port Renfrew during June, July and August, while during the current period Swiftsure and Nitinat during July and August were the most heavily sampled strata. Although dedicated SRKW surveys occurred in central Juan de Fuca and Sooke/Victoria during 2018 and 2019, no samples were collected. NOAA research programs have collected samples in these strata more recently (B. Hanson, pers. comm.), but those samples were not included here. No samples during the current period were included from central Juan de Fuca, Sooke/Victoria, or the San Juan Islands strata.

We attempted to fit various model structures to the SRKW prey remains data, but there were too few observations to adequately capture variability among seasons, spatial strata, and the early and current sampling periods. As a result, we provide a qualitative description of variability in stock composition. Fraser Summer 4_1 Chinook salmon were the most commonly observed stock, particularly in July and August. During the early sampling period, Fraser Spring 5_2, and to a lesser extent Summer 5_2, individuals were common in prey remains during June and July. The

Columbia Summer/Fall stock was regularly observed in the Swiftsure Bank and Port Renfrew strata, but were rare further east. The Puget Sound stock was observed throughout June, July, and August. ECVI-SOMN and WCVI stocks were relatively rarely observed.

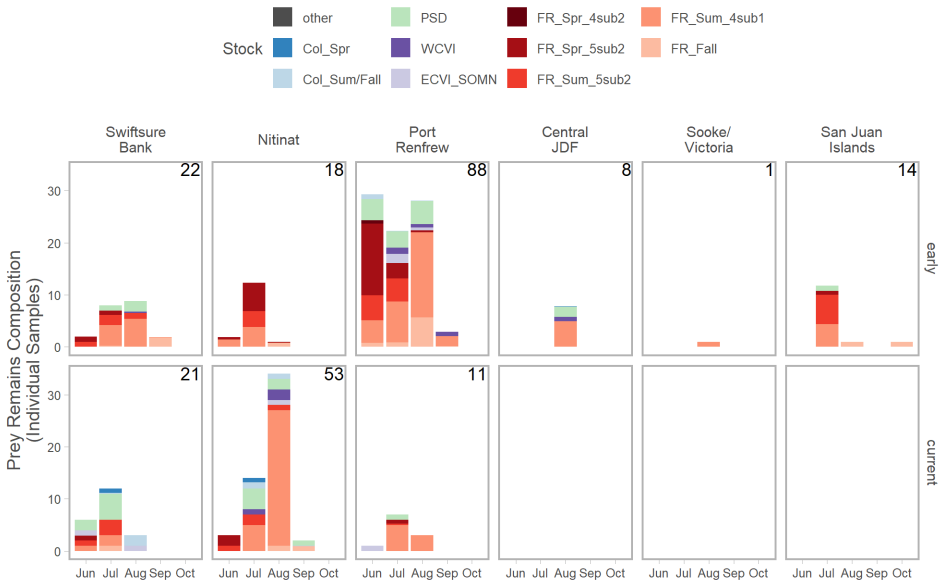

Figure 6. Monthly stock composition of Chinook salmon within SRKW prey remain samples. Strata (columns) correspond to spatial domains in Figure 2. Y-axis represents the number of samples collected in a given month-strata-sampling period. Numerals in upper right corner of each panel represent the total sample size in each strata and period.

The probability that hatchery-origin samples could be reliably identified in prey remains was relatively low because PBT marking rates did not exceed 80% in many hatcheries until the 2015 brood year or later (Figure A.4). Six prey remains samples belonged to populations and brood years with a PBT mark rate greater than 80%. Of these, three were stock identified based on PBT–two from the Robertson Creek (WCVI) and one from the Chilliwack (Fraser Fall) hatchery respectively. Four other prey remain samples were stock identified based on PBT, but came from population-brood years with mark rates less than 80%–one individual each from the Capilano (ECVI-SOMN), Puntledge (ECVI-SOMN), Big Qualicum (ECVI-SOMN), and Chilliwack hatcheries. One prey sample was identified with high certainty (>99%) as originating from Nitinat River (a WCVI population with a PHOS rate >75% in many years) during a year with a low PBT rate and therefore has a reasonably high probability of being hatchery origin. No other samples had a stock assignment that suggested a high probability of originating from Canadian hatcheries based on high (>75%) PHOS rates in recent years, though we note this is an uncertain classification technique.

The majority of prey remain samples were from ocean age-3 Chinook salmon. Ocean age-4 individuals were relatively common in the early sampling period, but more rarely observed in the current period. Few ocean age-2 and no ocean age-1 Chinook salmon were identified (Figure 7). Aging error, as well as variation among samples in age, stock identity, and sampling date resulted in additional variation in estimated body size (Figure 8). The probability that fish observed in the diets were smaller than 65 cm was very low across all months and strata, while $65 - 75$ cm individuals were relatively rare. In the early period, the probability that prey were in the

largest > 85 cm size bin was relatively high, while in the current period the $75 - 85$ cm size bin had the greatest probability. However, differences in when and where samples were collected prevent a quantitative test for changes in size composition.

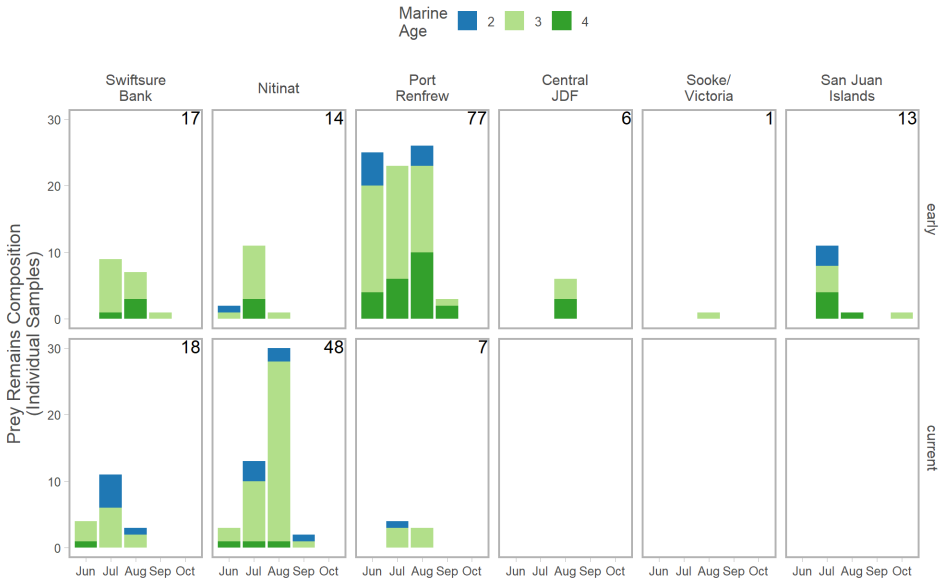

Figure 7. Monthly marine age composition of Chinook salmon within SRKW prey remain samples. Age data incorporate observation error associated with estimates from scale annuli. Strata (columns) correspond to spatial domains in Figure 2. Y-axis represents the number of samples collected in a given month-strata-sampling period. Numerals in upper right corner of each panel represent the total sample size in each strata and period.

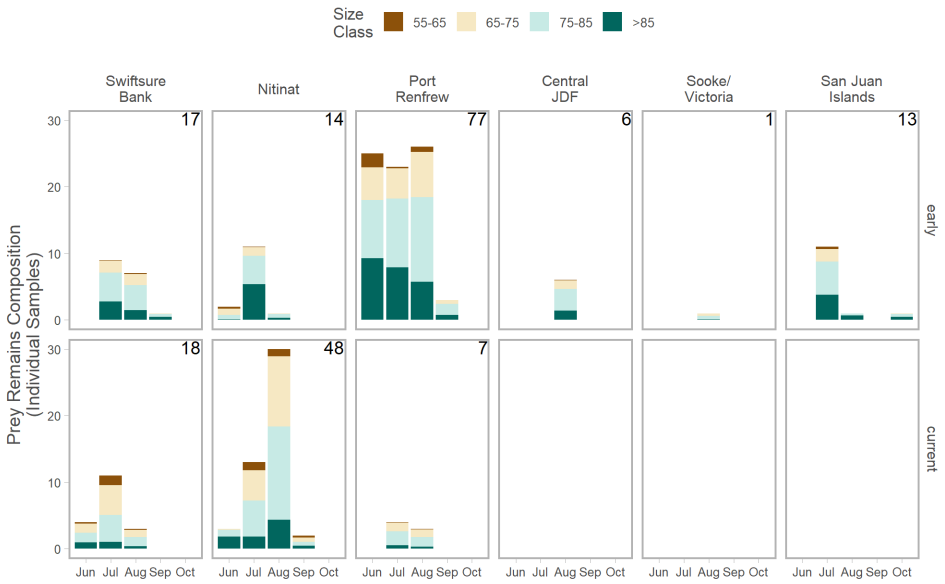

Figure 8. Monthly size class composition of Chinook salmon within SRKW prey remain samples based on predictions from season-specific size-at-age models (Appendix B). Strata (columns) correspond to spatial domains in Figure 2. Y-axis represents the number of samples collected in a given month-strata-sampling period. Numerals in upper right corner of each panel represent the total sample size in each strata and period.

3.2. RECREATIONAL CHINOOK SALMON FISHERIES

3.2.1. Stock Composition

There were 8,000 Chinook salmon samples that were collected from Chinook salmon that were (a) larger than 55 cm fork length, (b) caught between areas west of Juan de Fuca Strait and the southern Gulf Islands from 2014 to 2023, and (c) stock identified. The majority of recreational fishery samples were collected during summer months from locations within the Swiftsure Bank, Port Renfrew, and Victoria/Sooke strata (Figures 9, A.5). In strata where fishery samples were available across all seasons, stock composition transitioned from being dominated by the Puget Sound stock between November and May to a more mixed assemblage during the summer (Figure A.5).

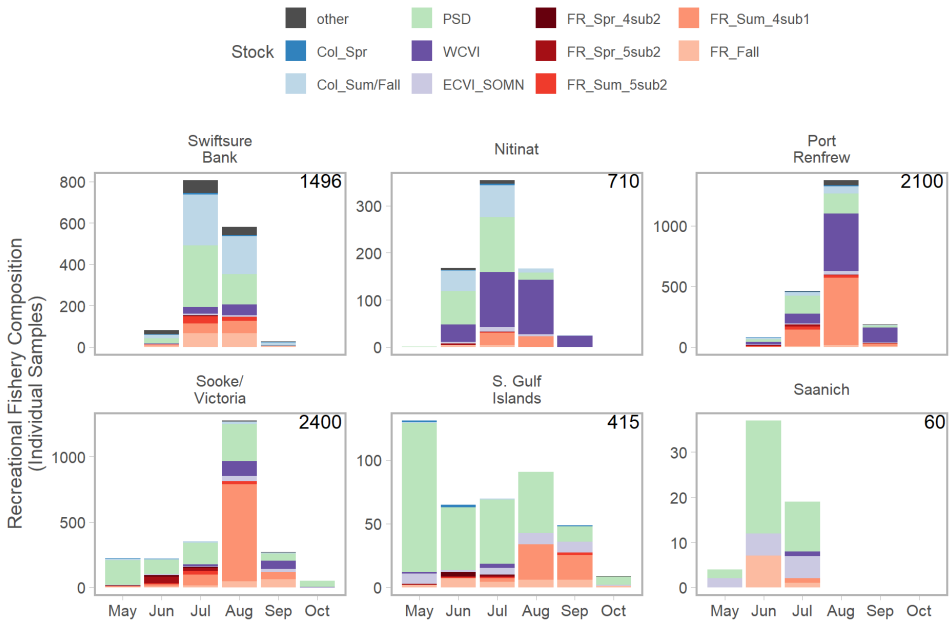

Figure 9. Monthly (May-October) stock composition of recreational Chinook salmon fishery samples. Strata (panels) correspond to spatial domains in Figure 2. Y-axis represents the number of samples collected in a given month and spatial strata. Numerals in upper right corner of each panel represent the total sample size in each strata.

Mean and variance in fork length differed among stocks (Figure 10). WCVI, Fraser Spring 5_2, Summer 5_2, and Summer 4_1 fish were typically larger (median lengths between 75 and 80 cm), while Puget Sound and ECVI-SOMN stocks were relatively smaller (median lengths less than 70 cm). The Fraser River Summer 4_1 stock had a more homogeneous size distribution (CV=0.09) than the Puget Sound, Columbia River Spring, Fraser River Fall, and ECVI-SOMN stocks (CV=0.12-0.13).

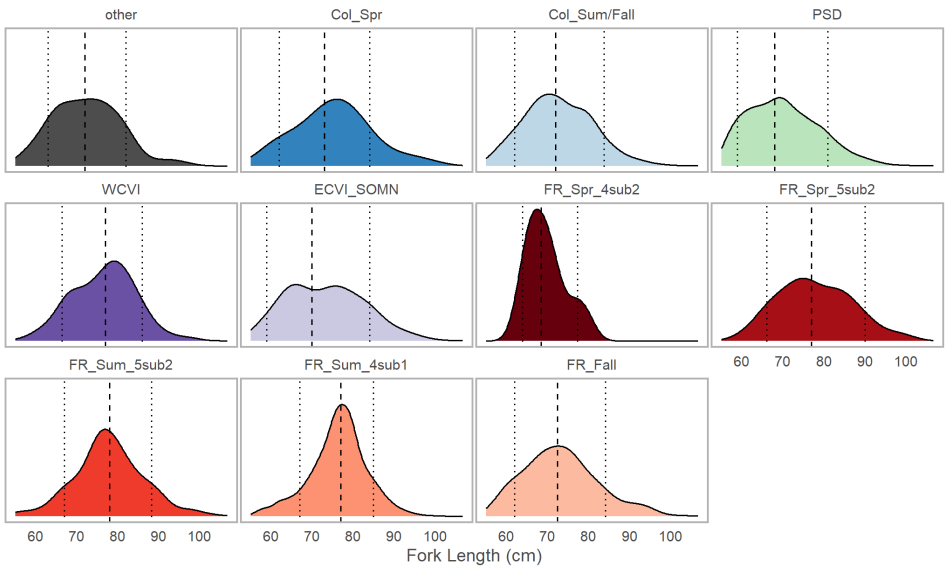

Figure 10. Kernel density estimates of observed stock-specific fork length (mm) of recreational Chinook salmon fishery samples (collected between May-October). Vertical lines represent stock-specific medians (dashed) and 80th percentile intervals (dotted). Note that samples smaller than 55 cm are excluded. Note y-axis scale differs among strata.

Our statistical model captured seasonal, spatial, and interannual variability in the relative abundance of Chinook salmon stocks, while accounting for uneven sampling effort. Chinook salmon stocks differed not just in mean relative abundance, but also seasonal trends in relative abundance. The relative abundance of Fraser yearling stocks (i.e., Spring 4_2, Spring 5_2, and Summer 5_2) declined over the course of the summer, while Puget Sound abundance declined over the summer then rebounded during September (Figure 11). Both Fraser Summer 4_1 and WCVI stocks reached maximum abundance in late summer, but with peaks several weeks apart, while the Fraser Fall stock peaked in late September (Figure 11).

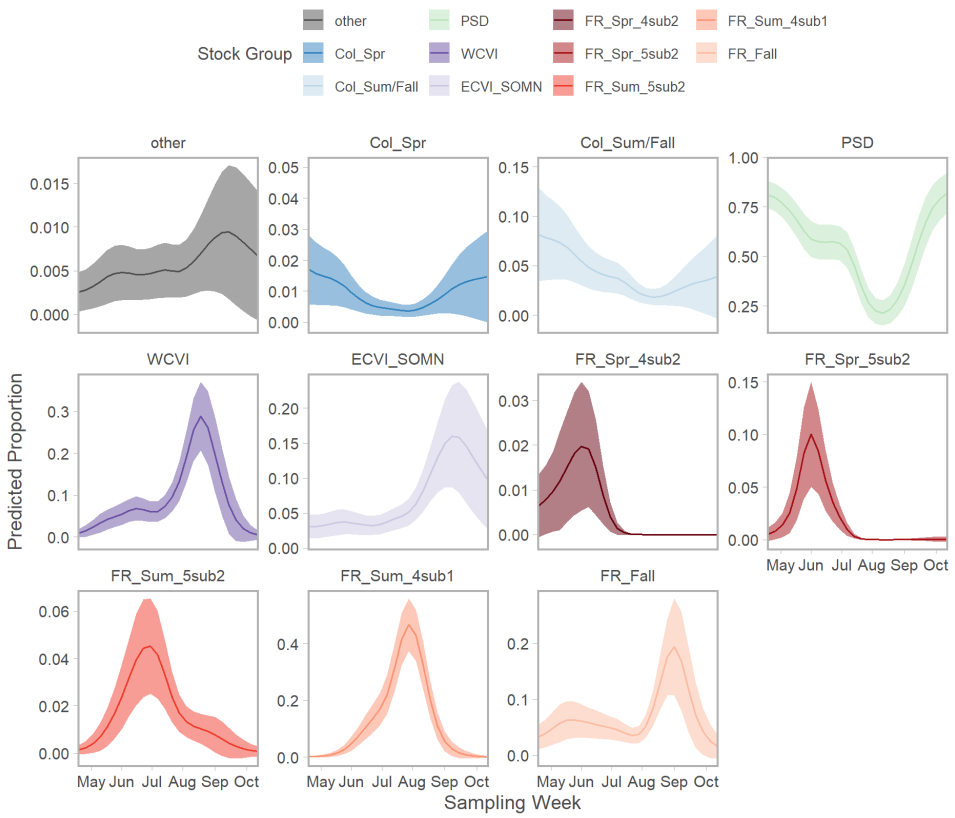

Figure 11. Predicted mean seasonal stock composition, based on a model fit to recreational fishery samples, from May to October. Ribbon represents 95% confidence interval of the mean prediction. Predictions represent conditional effects, excluding spatial covariates (i.e., represent the average seasonal effect within the study area). Note y-axis scale differs among stocks.

Stocks also showed unique spatial distributions. The 'Other', Columbia Spring, Columbia Summer/Fall, and Fraser Fall stocks were at their most abundant near the mouth of Juan de Fuca Strait and Swiftsure Bank, while the Puget Sound stock showed the opposite pattern (Figure 12). The WCVI stock was concentrated inshore, particularly near Nitinat Lake, while Fraser Spring 4_2, Spring 5_2, Summer 5_2, and Summer 4_1 stocks were most abundant in the middle of Juan de Fuca Strait (Figure 12). Unscaled predictions emphasize that stock composition, averaging among months May to October, varied spatially. Generally Columbia Summer/Fall and Puget Sound were the dominant stocks—the former on Swiftsure Bank and the latter in the southern Strait of Georgia (Figure 13). The WCVI stock was dominant in inshore locations near Nitinat Lake, while Juan de Fuca Strait had a more balanced stock composition due to the relatively high abundance of the Fraser Summer 4_1 stock (Figure 13).

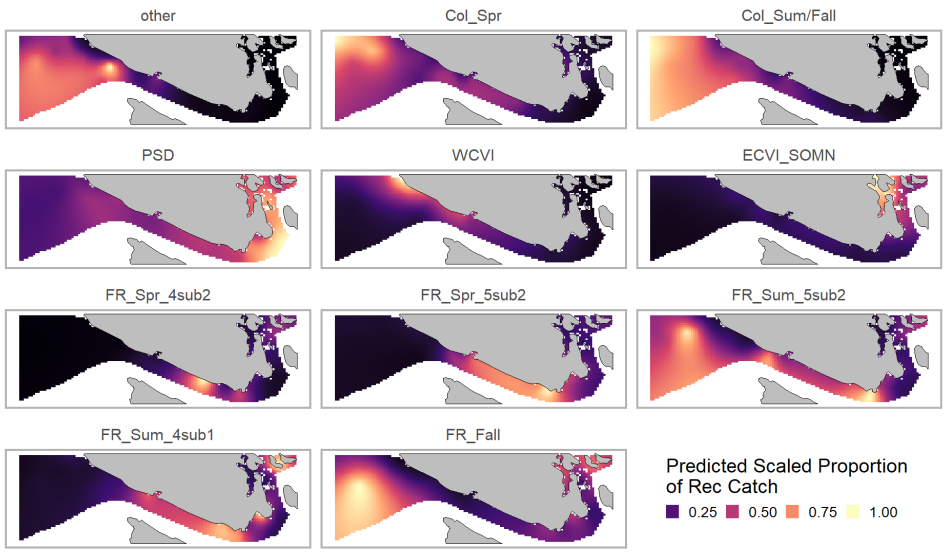

Figure 12. Spatial variation in scaled, predicted mean stock composition throughout Canadian portion of Juan de Fuca Strait and southern Strait of Georgia based on recreational fishery samples. Predictions are stock-specific averages for May through October and were scaled relative to the maximum prediction within a stock to emphasize stock-specific differences. A value of one (zero) indicates the location where a stock was at its maximum (minimum) predicted abundance.

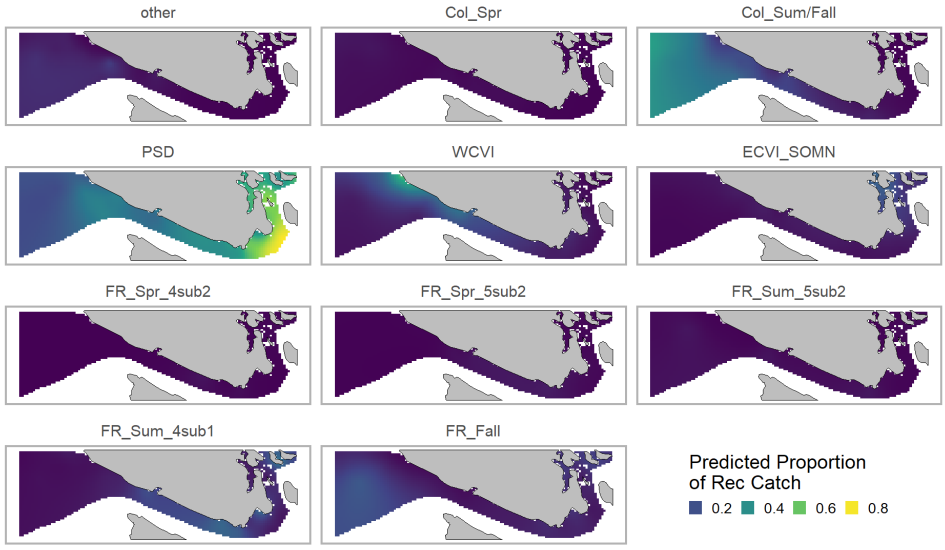

Figure 13. Spatial variation in predicted mean stock composition throughout Canadian portion of Juan de Fuca Strait and southern Strait of Georgia based on recreational fishery samples. Predictions are stock-specific averages for May through October. A value of one (zero) indicates a stock represented 100% (0%) of the predicted mean sample.

Seasonal predictions of mean stock composition for specific strata simultaneously highlight spatial and temporal variability in the relative abundance of different stocks (Figure 14). Near Swiftsure Bank, the Puget Sound and Columbia Summer/Fall stocks made up more than 90%

of the catch in June, but Fraser Summer 4_1 and WCVI stocks made up significant components of the catch as summer progressed. Nitinat showed a similar pattern, except with a much larger contribution of WCVI individuals, particularly in August and September when this stock made up more than 50% of the catch. The Port Renfrew and Sooke/Victoria strata showed the largest contribution of fish belonging to Fraser River stocks. Fraser-bound fish made up approximately 50% of the catch in August, predominantly the Summer 4_1 stock, but stocks with earlier run-timing were somewhat common in June. The Port Renfrew and Sooke/Victoria strata primarily differed in the proportion of the Puget Sound and WCVI stocks. The southern Gulf Island strata showed a similar stock composition to Sooke/Victoria, but included more ECVI/SOMN individuals.

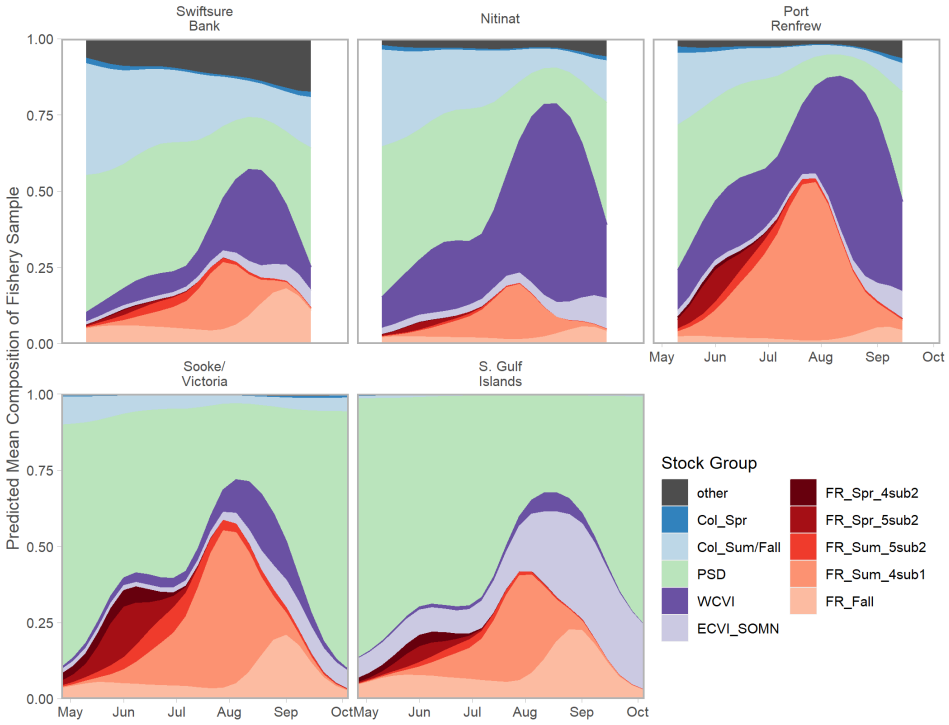

Figure 14. Predicted mean seasonal stock composition during summer months among five spatial strata based on recreational fishery samples. Predictions were estimated using locations (represented by an "x") within each spatial domain in Figure 2 and exclude interannual variability. Saanich not shown due to limited data in July and August, as well as its location outside SRKW critical habitat.

Interannual variability in relative abundance differed among stocks and spatial locations. Columbia River Spring, Puget Sound, and WCVI stocks were relatively stable compared to the remaining stocks (Figure A.6). For example, the predicted mean proportion of the sample belonging to Fraser River Summer 5_2 in Sooke/Victoria in July ranged from 4.6% to 17.7% among years.

The fitted model's residuals were appropriately distributed (Figure A.7) and posterior predictive checks confirmed simulated mean stock composition, accounting for residual variance, was generally similar to the observed stock composition (Figures A.8, A.9, A.10). However the hierarchical nature of the spatiotemporal models, which was necessary to generate predictions for a relatively large number of stocks, resulted in shrinkage that pulled individual observations towards the overall mean. As a result, observations from strata with relatively few samples, such as Saanich, and stock-strata combinations with strongly non-linear seasonal patterns (e.g., WCVI in Nitinat) deviated most strongly from model predictions.

3.2.2. Size Composition

We evaluated size composition using data from 10,651 Chinook salmon, larger than 55 cm fork length. Although the total sample size for the size composition analysis was larger, many samples were shared with the previously described stock composition dataset, resulting in a similar seasonal and spatial distribution of samples. Individuals smaller than 75 cm were relatively common in the Swiftsure Bank, southern Gulf Islands, and Saanich strata, while larger size classes were most abundant in Nitinat and Port Renfrew (Figure 15). In strata where samples were available across all seasons, fish larger than 75 cm were largely absent before May and after September (Figure A.11).

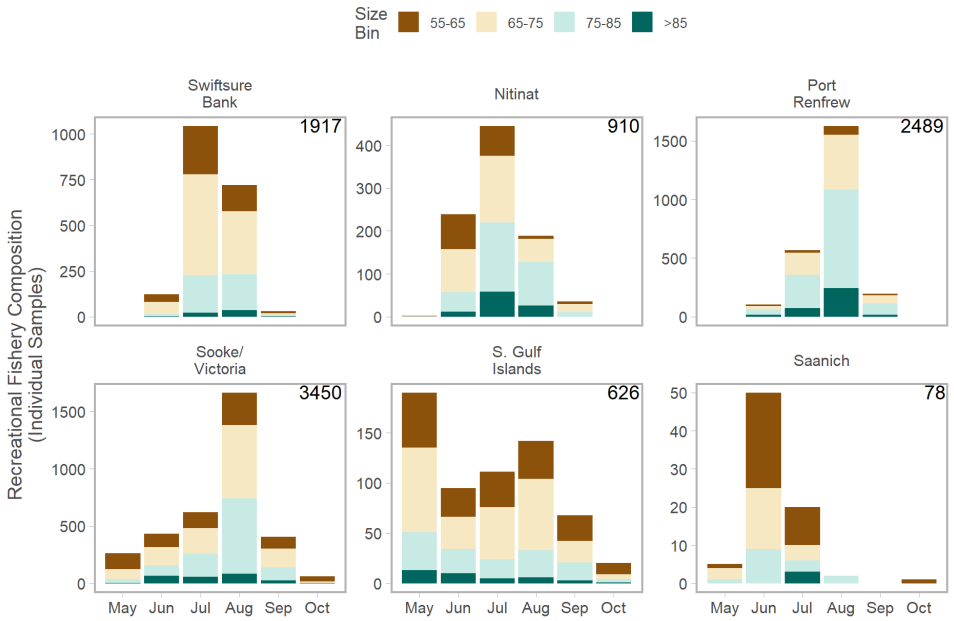

Figure 15. Monthly size composition of recreational Chinook salmon fishery samples during summer months. Strata (panels) correspond to spatial domains in Figure 2. Y-axis represents the number of samples collected in a given month and spatial strata (note scale differs among strata). Numerals in upper right corner of each panel represent the total sample size in each strata.

Chinook salmon size classes differed in average and seasonal abundance (Figure 16). The relative abundance of the 55-65 cm size class declined through the summer before increasing in September, while 75-85 cm individuals were most abundant in late July and August. The 65-75 cm and greater than 85 cm size classes were relatively more stable, though both declined in September (Figure 16).

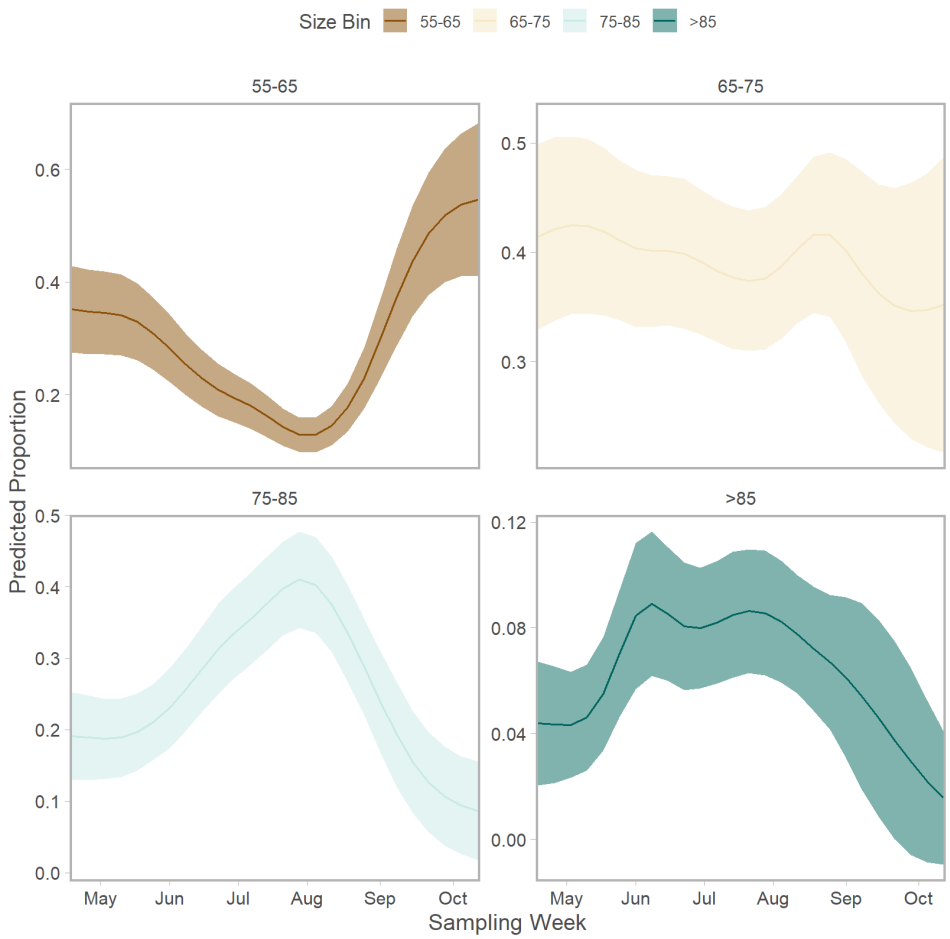

Figure 16. Predicted mean seasonal size composition based on recreational fishery samples. Ribbon represents 95% confidence interval of the mean prediction. Predictions represent conditional effects, excluding spatial terms (i.e., represent the "average" seasonal effect in the study area). Note y-axis scales differs among size classes.

Chinook salmon size classes showed different spatial distributions between May and October. The 55-65 cm size class reached maximum relative abundance near Victoria and Swiftsure Bank, while the relative abundance of the two largest size bins peaked inshore of Swiftsure Bank, as well as between Port Renfrew and Sooke. The 65-75 cm size class was more homogeneously distributed throughout the study area (Figure 17). Size composition shifted from being dominated by the 65-75 cm size class offshore and on Swiftsure Bank, to the 75-85 cm size class near Port Renfrew, and the smallest size class south of Victoria (Figure 18).

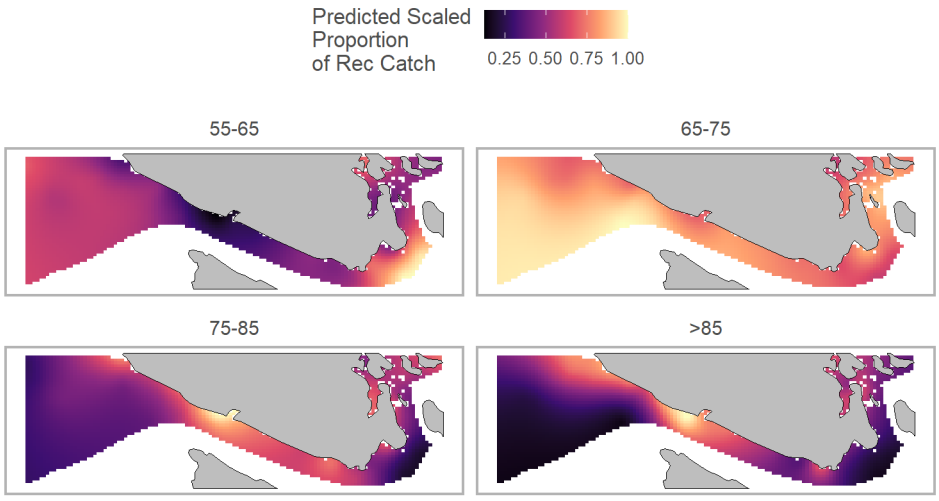

Figure 17. Spatial variation in scaled predicted mean size composition throughout Canadian portion of Juan de Fuca Strait and southern Strait of Georgia based on recreational fishery samples. Predictions are size class-specific averages for May through October and were scaled relative to the maximum prediction within a size class to emphasize size-specific differences. A value of one (zero) indicates the location where a size class was at its maximum (minimum) predicted abundance.

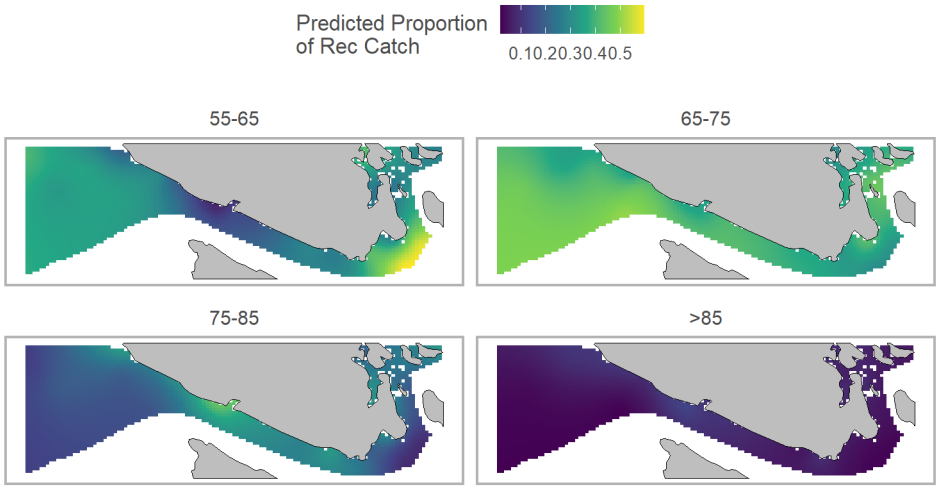

Figure 18. Spatial variation in predicted mean size composition throughout Canadian portion of Juan de Fuca Strait and southern Strait of Georgia based on recreational fishery samples. Predictions are size class-specific averages for May through October. A value of one (zero) indicates a size class represented 100% (0%) of the predicted mean sample.

As with stock composition, we used a spatiotemporal model to predict mean size composition throughout the summer for each strata. Swiftsure Bank and Nitinat had similar contributions of the smallest size class, but Nitinat had a relatively greater abundance of the two largest size classes (Figure 14). Port Renfrew had the relatively greatest contribution of the large size classes, with the mean predicted proportion of fish over 75 cm exceeding 65% in August. Further east, Sooke/Victoria and the southern Gulf Islands had seasonal patterns in size composition similar to Nitinat, though fish smaller than 55 cm were particularly abundant in Sooke/Victoria.

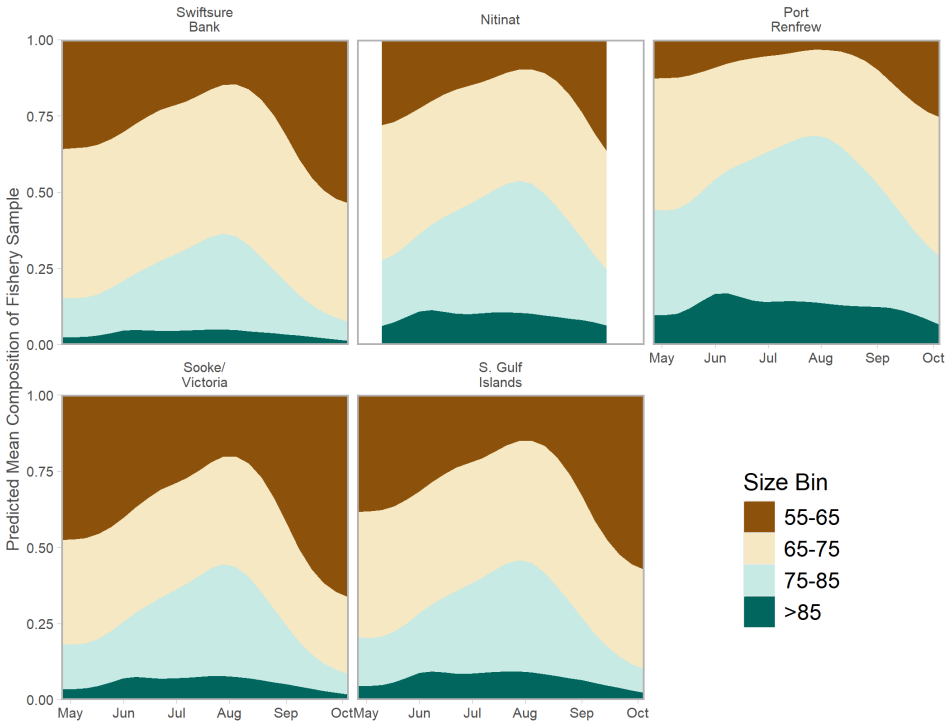

Figure 19. Predicted mean seasonal size composition during summer months among five spatial strata based on recreational fishery samples. Predictions were estimated using locations (represented by an "x") within each spatial domain in Figure 2 and exclude interannual variability. Saanich not shown due to limited data in July and August, as well as its location outside SRKW critical habitat.

The relative abundance of different size classes varied considerably among years (Figure A.12). For example, the predicted mean proportion of the sample belonging to the greater than 85 cm size class in Port Renfrew in June ranged from 7.7% to 20.9% among sampling years.

The fitted size composition model's residuals were appropriately distributed (Figure A.14) and posterior predictive checks confirmed simulated mean stock composition, accounting for residual variance, was generally similar to the observed size composition (Figure A.15). As with the stock composition model, the strongest deviations were in strata with relatively few samples (e.g., Saanich) or size classes and strata with strongly non-linear seasonal patterns (e.g., 55-65 cm in southern Gulf Islands).

3.2.3. Hatchery Contribution

From May to October, hatchery- or wild-origin status could be determined for most samples from the recreational fishery. Hatchery-origin individuals were relatively common in all strata, but

made up the majority of the catch in most months in the Swiftsure Bank, Nitinat, and Saanich strata (Figure 20). Conversely, wild-origin fish were relatively more abundant, particularly in August, in the Port Renfrew and Sooke/Victoria strata (Figure 20).

Figure 20. Relative abundance of hatchery- (green), wild- (purple), and unknown-origin (grey) individuals, grouped by country (Canada dark; USA light). Unknown assignments occurred when an individual with an intact adipose fin was assigned, based on GSI, to a stock without mass marking and incomplete parentage based tagging coverage.

Stocks differed in the relative contribution of hatchery-, wild- and unknown-origin individuals. The majority of individuals from American stocks were hatchery-origin (approximately 55-75%) and relatively few were unassigned because of the prevalence of mass marking in Washington and Oregon hatcheries (Figure 21). The contribution of hatchery fish to Canadian stocks was more variable and there was a greater proportion of individuals of unknown origin due to few Canadian hatcheries employing mass marking. Although PBT coverage is currently widespread in Canadian hatcheries, coverage has varied through time and was low prior to the 2013 brood year (Figure A.4). Thus many fish, particularly those captured prior to approximately 2017, could not be assigned a hatchery status reliably.

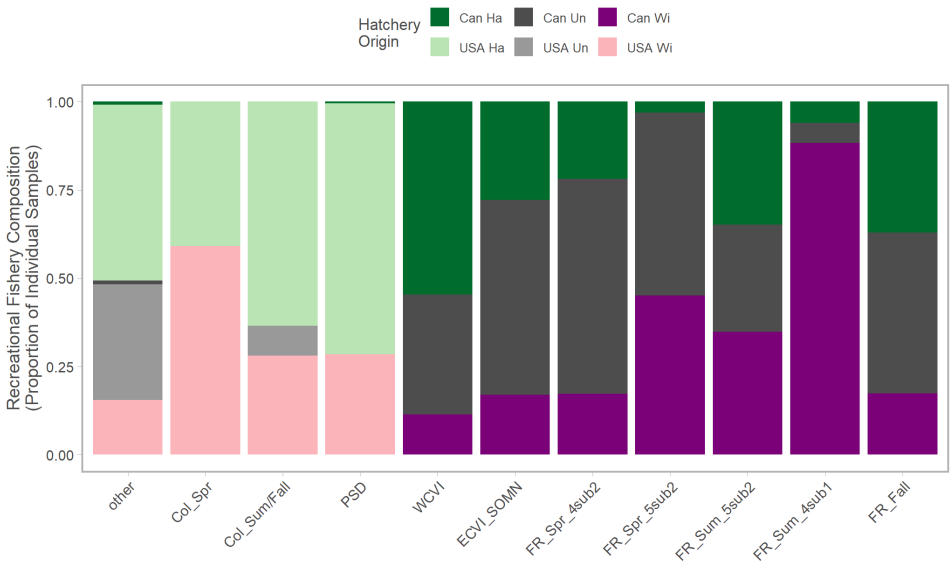

Figure 21. Relative abundance of hatchery- (green), wild- (purple), and unknown-origin (grey) individuals in each stock. Unknown assignments occurred when an individual with an intact adipose fin was assigned to a stock without mass marking or incomplete parentage based tagging coverage.

The proportion of hatchery-origin spawners (pHOS) between 2014 and 2022 differed among Canadian stocks and among years (Figure A.13). Mean pHOS was 72% among monitored populations in the WCVI stock and 53% for populations within the ECVI/SOMN stock. pHOS levels were slightly lower among Fraser River stocks, but most stocks had only one or two hatchery-enhanced populations (Figure A.13). There was considerable variability among populations within a stock, emphasizing that stock-level estimates of hatchery contributions based on pHOS alone should be interpreted cautiously.

3.3. SELECTIVITY IN SRKW PREY REMAINS

We used Monte Carlo simulations to test for evidence that the observed stock and size composition of SRKW prey remains (collected after 2016 and in the Swiftsure Bank, Nitinat, and Port Renfrew stratas) deviated from the expected composition as indexed by the recreational fishery. Our approach accounted for spatial, seasonal, and interannual variability by using the previously described composition models, while propagating uncertainty due to genetic stock assignment, age assignment, small sample sizes, and estimated model parameters.

We found evidence of positive selection for the Fraser River Spring 5.2, Summer 5.2, and Summer 4.1 stocks (Figure 22). These stocks made up 4-36% more of the observed prey remains sample than predicted by the stock composition model parameterized with recreational fishery data. Conversely, the WCVI, Puget Sound, Columbia Summer/Fall, and ‘Other‘ stocks were underrepresented in prey remains, with their proportional contribution 5-27% less than the model prediction (Figure 22). There was no evidence of selectivity in the remaining stocks, likely because their observed relative abundance was low in both the prey remains and predicted to be low at the times and locations where prey remains were collected (Figures 6, 14).

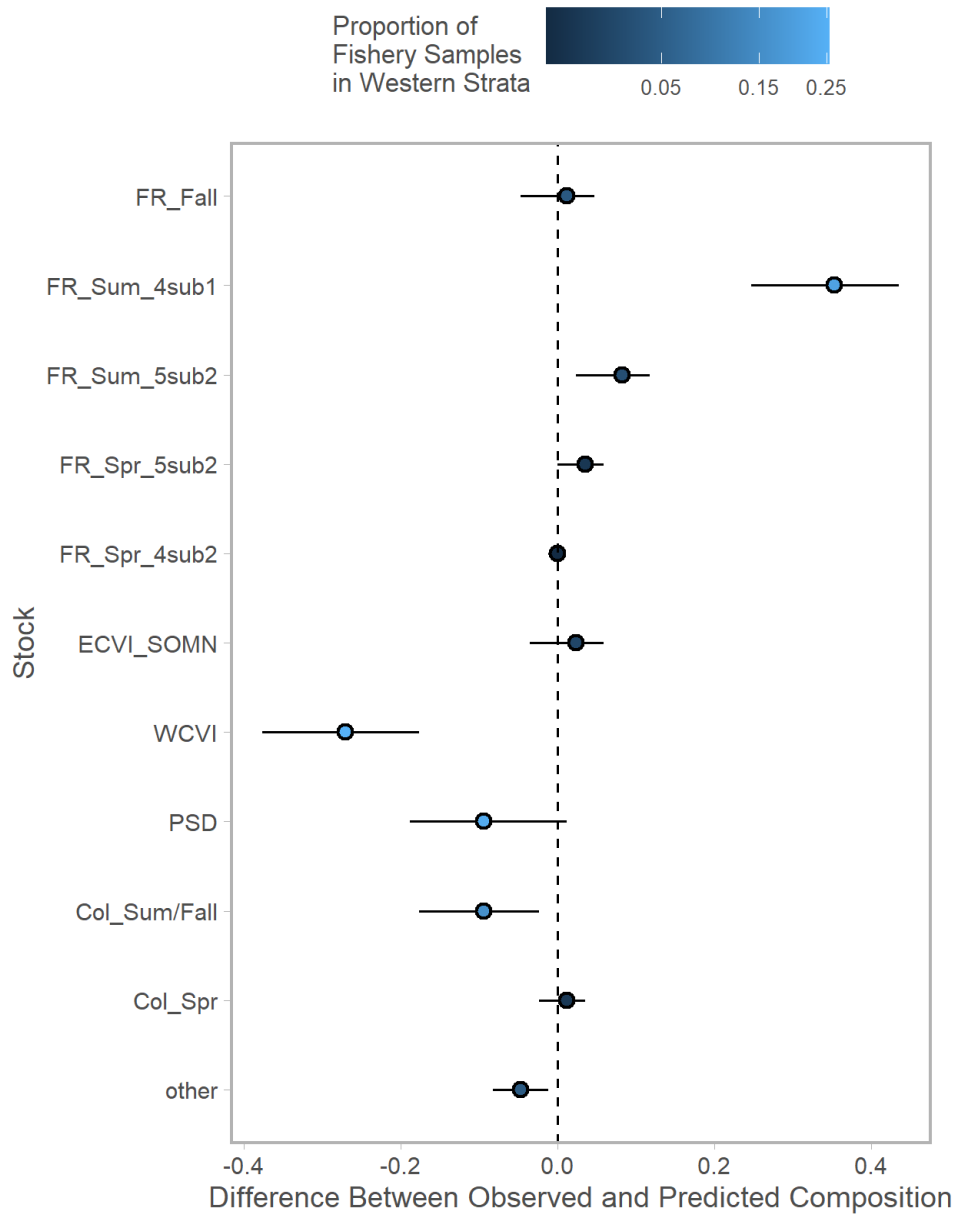

Figure 22. Differences between the observed and model predicted contribution of each stock to SRKW prey remains. Positive (negative) values indicate a given stock was observed more (less) frequently in SRKW prey remains than predicted by the fishery-dependent model. Points represent medians and whiskers represent 95th percentile intervals among 500 Monte Carlo simulations. Brighter (darker) points represent stocks that were more (less) common in recreational fishery samples from times and strata coincident with SRKW prey remains.

The two smallest Chinook salmon size classes made up a smaller proportion (approximately 10% and 7% respectively) of the observed prey remains than predicted by the size composition model parameterized with recreational fishery data (Figure 23). We also found evidence of positive selection for the two largest size classes, which were approximately 8% more common in the observed prey remains than predicted by the model (Figure 23). Selectivity estimates for the

two intermediate size classes (65-75 and 75-85 cm) were more uncertain than the other two size classes despite similar medians (Figure 23).

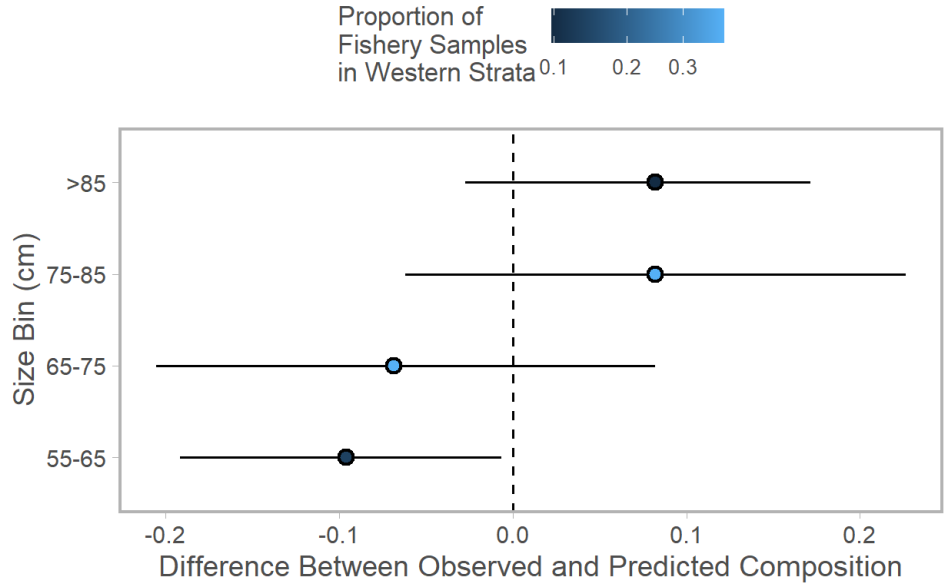

Figure 23. Differences between the observed and model predicted contribution of each size class to SRKW prey remains. Positive (negative) values indicate a given size class was observed more (less) frequently in SRKW prey remains than predicted by the fishery-dependent model. Points represent medians and whiskers represent 95th percentile intervals among 500 Monte Carlo simulations. Brighter (darker) points represent size classes that were more (less) common in recreational fishery samples from times and strata coincident with SRKW prey remains.

3.4. SENSITIVITY ANALYSES

The stock composition model that was fit to data that only included recreational fisheries samples greater than 75 cm fork length predicted slightly different stock composition, particularly early in the year (Figures D.1, D.2). However, the same stocks showed evidence of positive and negative selectivity (Figure D.3). Similarly, stock selectivity and size selectivity results were similar when samples that overlapped with fisheries management interventions were excluded. Additional details in Appendix D.

3.5. CHINOOK SALMON TERMINAL ABUNDANCE

All Chinook salmon stocks present in the study area have shown cyclical trends in terminal abundance over the past 40 years; however, these dynamics have not been homogeneous. Washington and Oregon Coastal (included in the 'Other' stock throughout this analysis); Columbia River Spring; and Fraser River Spring 4_2, Spring 5_2, and Summer 5_2 stocks declined through the 2010s and have shown variable degrees of recovery (Figure 24). Conversely, the terminal abundance of WCVI, ECVI/SOMN, and Fraser River Summer 4_1 stocks has increased (Figure 24).

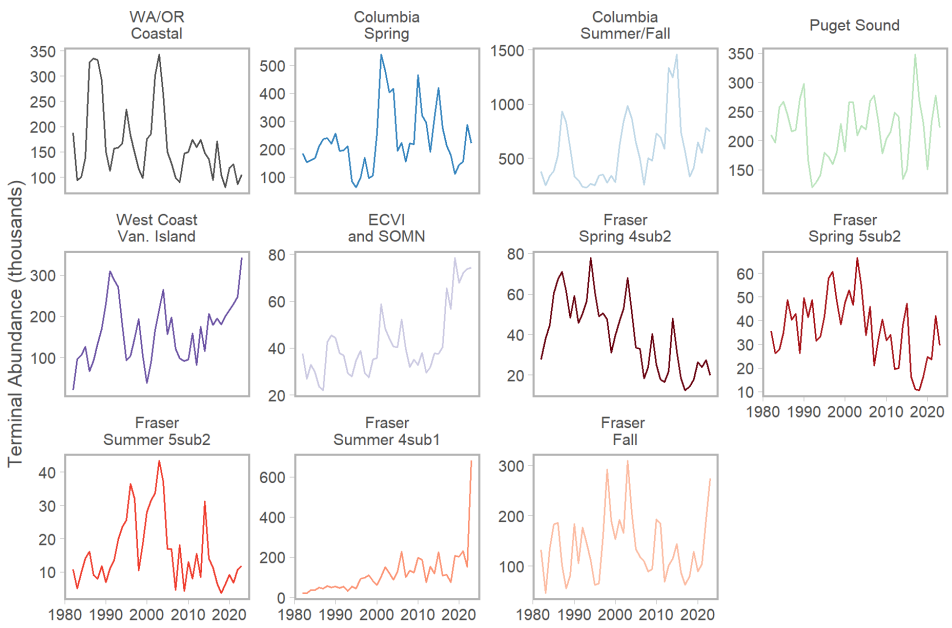

Figure 24. Terminal abundance of Chinook salmon stocks. Washington and Oregon (WA/OR) Coastal populations are included in the 'Other' stock throughout this manuscript. 2023 data were unavailable for WA/OR Coastal and Puget Sound stocks and were imputed based on 2019-2022 averages. Y-axis scales differ among stocks. Definitions of terminal abundance and data sources available in Appendix C.

Aggregate (i.e., summed among stock) terminal abundance has also varied cyclically, but is relatively high compared to terminal abundance prior to 2000 (Figure 24). Generally the majority of aggregate terminal abundance originates with outer coast stocks (Washington and Oregon Coastal, Columbia River, West Coast Vancouver Island); however, the contribution of stocks that spawn in Salish Sea watersheds has increased in recent years.

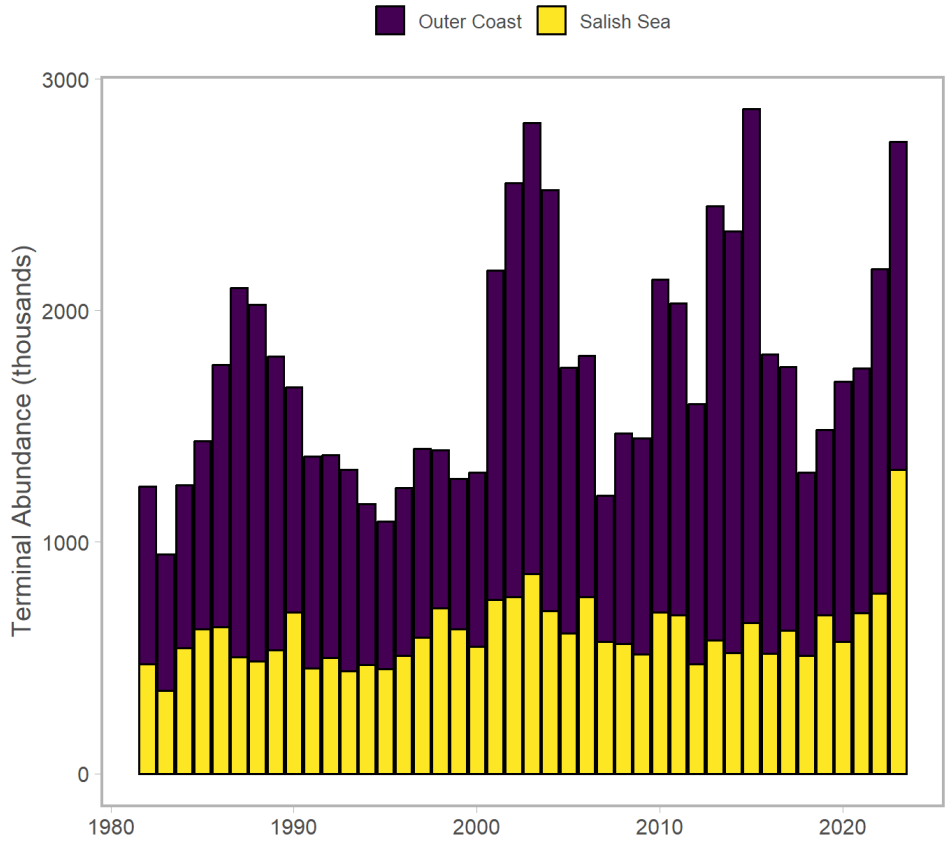

Figure 25. Aggregate terminal abundance of Chinook salmon stocks, common in SRKW critical habitat, spawning inside the Salish Sea (yellow) or in Outer Coast, including the Columbia River (purple). Lightly shaded bars represent five-year mean values. 2023 is not shown given missing data for Washington Coastal and Puget Sound stocks. Definitions of terminal abundance and data sources available in Appendix C.

4. DISCUSSION

Our understanding of the relationship between SRKW and Chinook salmon has evolved over the last five decades. From the identification of the "resident" fish-eating ecotype (Ford and Ellis 2006) to the correlation between coastwide Chinook salmon abundance indices and resident killer whale mortality (Ford et al. 2010*a*), the importance of Chinook salmon as a primary prey is undisputed. However, variability in the abundance and seasonal distribution of stocks contributing to coast-wide Chinook salmon indices, as well as the likely influence of other threats, have clouded the relationship between Chinook abundance and SRKW population dynamics (Nelson et al. 2024, Saygili and Trites 2024, Vélez-Espino et al. 2015).

In this study, we leveraged samples from SRKW prey remains and recreational fisheries, both collected within SRKW critical habitat in southern British Columbia, to explore three interrelated questions. First, which Chinook salmon stocks and size classes are most commonly observed in SRKW diets? Second, what is the composition of the prey field available to SRKWs, particularly in locations where prey remains data are limited? Third, is there evidence of stock- or size-selective foraging by SRKWs? We frame our results in the broader context of changes in Chinook

salmon abundance, variability in hatchery supplementation among stocks, and potential drivers of selectivity by SRKW. Finally, we link our results to potential management actions that may improve Chinook salmon availability for SRKW. Recognizing differences between observed diets and the available prey field provides a necessary degree of granularity with which to view opportunities for refined management options in support of SRKW prey needs.

4.1. COMPOSITION OF SRKW PREY REMAINS

Samples from SRKW prey remains collected during summer months between Juan de Fuca Strait and the San Juan Islands were dominated by a subset of Fraser River Chinook salmon stocks. Fraser Spring 5_2 and Summer 5_2 fish, stocks with a yearling life history and early run-timing, were relatively abundant in June and July, while subyearling Fraser Summer 4_1 individuals were the dominant component overall, particularly in July and August. The remaining stocks were observed at relatively low abundance. There was some evidence that yearling, early-run stocks made up a smaller proportion of the diet in the current period than the early period; however, we could not test that hypothesis due to differences in the timing and location of sampling. Although we could not reliably identify hatchery-origin Chinook salmon in SRKW prey remains, seven samples were identified based on PBT and originated from lower Fraser River Fall, ECVI, and WCVI hatcheries.

We also evaluated the size composition of SRKW diets, using scales to estimate the mean fork length of sampled prey remains based on size-at-age relationships. Chinook salmon predicted to be smaller than 65 cm fork length were largely absent from the age-identified samples, which were instead dominated by 75-85 and >85 cm size classes. These patterns are consistent with previous summer observations from the Salish Sea that found interior Fraser River populations and older age classes were major components of SRKW diets (Ford and Ellis 2006, Hanson et al. 2010).

Too few prey remains samples were collected to statistically account for variability among sampling periods, sampling weeks, and spatial locations. Though observations from locations and months with a larger number of samples are more reliable than those with fewer, without a model we cannot present reliable uncertainty estimates or determine the minimum sample size necessary to draw inference reliably (e.g., Trites and Joy 2005). We caution against assuming SRKW diets in locations or months without samples will be similar to observations elsewhere given seasonal and spatial variability in Chinook salmon stock and size composition.

4.2. COMPOSITION OF THE RECREATIONAL FISHERY

Chinook salmon stocks differ in distribution, physical characteristics, and freshwater migration timing (Healey 1991, Weitkamp 2010), resulting in substantial spatial and seasonal variability in stock-specific abundance within marine habitats (Freshwater et al. 2021, Shelton et al. 2019). We leveraged a large number of samples collected from Canadian recreational fisheries to quantify variability in Chinook salmon stock and size composition at particularly fine scales. We found marked differences in the composition of the recreational fishery among sampling weeks within a location and between locations five to ten kilometers apart within a sampling week.

A primary driver of temporal variation in Chinook salmon stock composition is the relative contribution of resident stocks, which are present in southern continental shelf habitats year-round, and migratory stocks that become more abundant as mature individuals migrate towards freshwater habitats. For example, the Puget Sound stock is present in the Salish Sea year-round (Freshwater et al. 2021, O'Neill and West 2009), and dominated the composition of recreational fisheries,

particularly early in the summer. Conversely, Fraser River stocks, with the exception of fall-run individuals, typically migrate north along the continental shelf or offshore (CTC 2022). The stock composition showed successive peaks as returning Spring 4_2, then Spring 5_2, Summer 5_2, and Summer 4_1 spawners migrated towards the Fraser River. WCVI individuals, which typically mature in Alaskan waters (Shelton et al. 2019), and Fraser River Fall individuals, which are resident along the shelf and within the northern Strait of Georgia, were abundant in specific locations in late summer. Notably Columbia River Spring individuals were rare, even in outside areas, suggesting this stock may migrate further offshore until reaching the Columbia River.

Spatial patterns also differed among stocks. WCVI individuals were largely constrained to nearshore waters from Nitinat Lake to Port Renfrew. Columbia River Summer/Fall individuals were abundant from Swiftsure Bank west towards La Perouse Bank. This region also included a relative large contribution of Fraser River Fall fish, consistent with recent trawl bycatch data (Lagasse et al. 2024), and indicating it may be a rearing area for this stock. Fraser River Summer 4_1 individuals were most abundant in Juan de Fuca Strait. Finally, Puget Sound individuals were widespread from Swiftsure east to the southern Strait of Georgia, but were most dominant in inshore areas.

Differences in size composition are associated with stock composition because Chinook salmon vary in size- and age-at-maturity (Healey 1991), but they also reflect ontogenetic differences as fish continue to grow over summer and show changes in habitat use (Freshwater and King 2024, Freshwater et al. 2024). Generally fish smaller than 65 cm were most abundant early and late in the year, before and after spawning individuals have migrated through the area. The 75-85 and >85 cm size classes showed the opposite pattern, while the 65-75 cm size class showed weak seasonal variability. The two larger size classes are predominantly mature fish, but the latter includes both sexually mature fish, as well as individuals who will remain at sea for an additional year (Freshwater and King 2024, Freshwater et al. 2024). Spatial patterns also supported this hypothesis—fish smaller than 75 cm were widespread and particularly abundant offshore of Swiftsure Bank and south of Victoria, locations commonly considered rearing habitat for resident fish, while those larger than 75 cm were concentrated near the mouth of Juan de Fuca Strait. Hot spots of abundance for larger size classes were similar to locations where SRKW foraging behaviours are most commonly observed (Thornton et al. 2022).

Estimates of stock and size composition have the potential to be strongly influenced by management measures such as mark selective fisheries and size limits. While it was not possible to statistically account for these influences, our results do not map uniformly onto the timing and location of management interventions. For example, gradual changes in stock and size composition throughout the summer, rather than knife-edge transitions associated with a change in fishing regime, were present in strata such as Sooke/Victoria that have had maximum size limits in place during the summer for the entire time series. Swiftsure Bank, Sooke/Victoria, and the southern Gulf Islands showed similar patterns in size composition to one another despite very different management regimes. Finally, Nitinat had a smaller size distribution than Port Renfrew despite much less restrictive management interventions. Thus while the impact of management interventions on composition estimates is unlikely zero, it is also unlikely that they are solely responsible for seasonal and spatial variation. We explore these factors in additional detail in the Limitations section.

4.3. RELATIVE ABUNDANCE OF HATCHERY-ORIGIN FISH

Providing accurate estimates of the relative abundance of hatchery-origin fish in SRKW prey remains and critical habitat is challenging. Data from the prey remains themselves can only

be assigned as hatchery-origin with relatively high certainty based on PBT. Yet estimates of hatchery contributions to the diet based on PBT alone will be biased low because PBT assignments are unavailable for American stocks and PBT coverage varied among years and among hatcheries for Canadian stocks as the method was gradually introduced.

The accuracy of hatchery contribution estimates for fisheries-dependent samples is higher because hatchery individuals can be identified based on missing adipose fins. Since adipose clip rates are relatively high in Washington and Oregon hatcheries (Anderson et al. 2020, ODFW 2022, WDFW 2021), American-origin fish could normally be reliably assigned. Canadian mark rates, however, are much lower and unmarked Canadian fish that belonged to a brood year with a low PBT rate could not be reliably identified as hatchery- or wild-origin. The Salmonid Enhancement Program (the DFO program responsible for hatchery operations) quantifies one dimension of hatchery impacts by estimating the proportion of hatchery-origin individuals on the spawning grounds (pHOS). Yet only a subset of populations within each stock are assessed and pHOS estimates do not reflect hatchery abundance in returns to enhancement facilities or in harvest. Thus, it is not possible at this time to derive an index of the relative abundance of hatchery fish within a given Canadian stock, particularly during marine residence where multiple cohorts co-occur.

4.4. SRKW FORAGING BEHAVIOUR

Evaluating SRKW prey availability requires a nuanced understanding of SRKW foraging needs and foraging behaviour. Killer whale populations exhibit rigorous ecological specialization (Riesch et al. 2012), which reduces competition (Whitehead and Ford 2018). In killer whales, this focus on a small portion of the resource spectrum supports the co-existence of three ecotypes within Canadian Pacific waters (resident, transient, and offshore killer whales). While behavioural specialization reduces competition and favours survival when prey is not limiting, highly specialized prey selectivity may be detrimental to a population's survival when primary prey populations are less abundant, as evidenced by the SRKW population.

Although the cultural specificity of SRKW prey selection appears to be rigid, the population does show changes in foraging behaviour and spatial distribution that are consistent with a response to prey availability. Winter diet data indicate a relatively high prey species diversity, likely in response to lower seasonal densities of Chinook salmon (Hanson et al. 2021); however, Chinook salmon remain a large component of the diet throughout the year (Van Cise et al. 2024). In concert with the increased diversity in winter prey selection, SRKW movements are also more irregular and expand throughout their range (Hanson et al. 2017). Seasonal site fidelity appears to be correlated with increasing Chinook salmon abundance, beginning in late March with increased use of habitats near the mouth of the Columbia River (Hanson et al. 2017, Zamon et al. 2007). By early June, SRKWs are more common in the vicinity of Swiftsure Bank (Thornton et al. 2022), and their use of southern BC habitats continues to grow throughout the summer (Ettinger et al. 2022, Stewart et al. 2023). Critically, SRKW physical condition covaries with seasonal movements and typically is poorest in spring and early summer, then recovers during late summer and autumn (Fearnbach et al. 2020; J. Durban, pers. comm.). Seasonal trends in physical condition are likely associated with a reduction in the contribution of Chinook salmon to SRKW diets and increased energy expenditure to forage on a more diverse and less spatially concentrated prey base. We note that these patterns reflect SRKW behaviour over recent decades, which may have diverged from historical patterns due to large reductions in the SRKW population

size, as well as changes in the relative abundance of specific Chinook salmon stocks (e.g., Fraser River yearling populations).

4.5. SRKW SELECTIVITY

While co-occurrence of predator and prey is a prerequisite of foraging, predators may select prey disproportionately to their abundance. We found broad similarities between the stock composition of SRKW prey remains and the fishery-dependent data, including a seasonal decline in Fraser River Spring 5_2 and Summer 5_2 stocks, a seasonal increase in the Fraser River Summer 4_1 stock, and the persistent presence of the Puget Sound stock. Yet temporal and spatial variability in Chinook salmon stock and size composition interact to produce a variable prey field for SRKW, even at the relatively small scales over which prey remains were collected here. To account for spatiotemporal variability in Chinook salmon composition, as well as uneven sampling of SRKW prey remains, we used a simulation model to test for evidence that specific stocks and size classes were present in prey remains disproportionately to their abundance as indexed by the fishery.

SRKW showed positive selection for Fraser Spring 5_2, Summer 5_2, and Summer 4_1 stocks, as well as negative selection towards WCVI, Columbia Summer/Fall, Puget Sound, and 'Other' stocks. Differences between prey remains and fishery-dependent samples were negligible for the remaining stocks after propagating sampling, stock identification, and model uncertainty. Additionally, SRKW showed a gradient of size selectivity. The smallest and largest size classes were under- and overrepresented, respectively, in diets relative to the recreational fishery. Selectivity for the intermediate size classes was similar directionally, but more uncertain.

Our results are consistent with evidence that SRKW preferentially target larger and older Chinook salmon as prey, presumably to maximize energetic returns per prey item (Ford and Ellis 2006, O'Neill et al. 2014). However, several stocks with the largest body size (Fraser Spring 5_2, Fraser Summer 5_2, Fraser Summer 4_1, and WCVI) showed evidence of both positive and negative selectivity in SRKW prey remains. Stock selectivity was also still present after we constrained our analysis to the largest Chinook salmon size classes (Figure D.3).

Our first hypothesis is that variability in lipid content, as well as body size, influences prey value. Typically Chinook salmon undergoing longer spawning migrations to interior watersheds have higher lipid content, per gram of body weight, than coastal populations migrating shorter distances (Quinn 2018). Among-stock differences in lipid content are present in terminal marine and freshwater habitats once spawning migrations have begun (Lerner and Hunt 2023, O'Neill et al. 2014), but also in non-terminal marine areas where both Chinook salmon and SRKW are actively foraging (Freshwater and King 2024, Hendriks 2024). In these marine areas, Fraser River Spring 5_2 and Summer 5_2 stocks have a lipid content approximately 10% higher (per unit body mass) than Fraser River Summer 4_1 or Upper Columbia River and Snake River Summer/Fall stocks, 20% higher than Fraser River Fall, Puget Sound, or lower Columbia River Fall stocks, and 30% higher than the WCVI stock (Freshwater and King 2024). Generally stocks with evidence of positive selectivity in SRKW prey remains were those that migrate to interior watersheds, while those with negative selection are more likely to include subyearling populations that migrate shorter distances to coastal spawning locations. There was neutral selectivity towards several spring-run stocks with interior spawning populations, which could be due to their smaller mean size (Fraser River Spring 4_2) or very low proportional abundance resulting in limited statistical power.

While variation in lipid content is a parsimonious explanation, it is possible stock selectivity is influenced by other factors. Selection of an individual Chinook salmon by SRKWs may be

influenced by the location of the fish in the water column (Wright et al. 2017), the ambient noise environment (Tennessen et al. 2024), and bathymetric features that interfere with the receipt of an echolocation signal (e.g., substrate composition, rugosity). These factors may reduce prey accessibility through decreased effectiveness of echolocation or by reducing the likelihood of a successful pursuit.

Differences among Chinook salmon in the use of habitats that vary in these traits may determine their availability as prey. For example, vertical distributions differ among Chinook salmon stocks due to unique migratory pathways or differences in the relative proportion of mature and immature individuals (Freshwater et al. 2024). WCVI Chinook salmon staging in terminal areas are bottom oriented and may be less likely to exhibit foraging behaviours that expose them to SRKW predation (e.g., Walters and Juanes 1993). On the other hand, Fraser River bound fish appear to migrate more rapidly through the Salish Sea than Puget Sound individuals (Hendriks 2024), which intuitively might reduce their availability as prey—the opposite of our selectivity results. While our simulation accounted for differences among stocks in spatial distribution, it is not suitable for evaluating granular patterns in habitat use. Future research aimed at understanding stock-specific Chinook salmon behaviour and physiology may be necessary to understand patterns of SRKW selectivity.

Finally, our results may be influenced by fishery selectivity independently of SRKW selectivity. We evaluate this possibility in the Limitations and Future Research Directions section.

4.6. MANAGEMENT IMPLICATIONS

The value of different Chinook salmon stocks as prey to SRKW may be influenced by at least three characteristics: lower SRKW physical condition during spring, the nutritional quality of different Chinook salmon stocks, and spatio-temporal overlap between Chinook salmon and SRKW foraging habitats. Given these assumptions, as well as divergent trends in abundance among Chinook salmon stocks, we suggest prey availability for SRKW in Canadian critical habitat could be maximized by meeting two objectives—increasing the abundance of at-risk Fraser River Spring 5_2 and Summer 5_2 stocks and increasing the body size or energy density of relatively abundant subyearling stocks that are present in SRKW foraging habitats.

Fraser River Spring 5_2 and Summer 5_2 individuals may be particularly important prey items during the spring and early summer period because their migration occurs after Columbia River Spring populations, but before that of the relatively more abundant Columbia River Summer/Fall, Fraser River Summer 4_1, and Fraser River Fall stocks (Jepson et al. 2010, Keefer et al. 2004, Parken et al. 2008). Both Fraser River Spring 5_2 and Summer 5_2 individuals were present in SRKW prey remains disproportionate to their abundance, consistent with previous evidence that indiviudals from these stocks are common prey (Hanson et al. 2010). Both stocks are also lipid-rich and large bodied (Xu et al. 2020, Lerner and Hunt 2023, Freshwater and King 2024, this study). Finally, the abundance of Fraser River Spring 5_2 and Summer 5_2 populations has declined relative to historic levels (COSEWIC 2018, DFO 2020, 2021) and other, more abundant stocks present in critical habitat early in the year are typically smaller and have lower mean lipid content (Freshwater and King 2024, Freshwater et al. 2021, Hendriks 2024, O'Neill et al. 2014).

Yet there are limited options to rapidly increase the abundance of the Fraser River Spring 5_2 and Summer 5_2 stocks. Canadian marine exploitation rates have been low for several years (DFO 2023*a*). No Spring 5_2 or Summer 5_2 populations currently have large-scale enhancement programs (defined here as greater than 140,000 juvenile releases per year (DFO Salmon Enhancement Program, unpublished data)). It is beneficial to continue diverse efforts to rebuild these stocks

via habitat restoration, reduced harvest pressure, and targeted enhancement via small-scale conservation hatcheries even if they are unlikely to increase abundance in the short-term.

While many yearling Chinook salmon stocks have declined in abundance, the abundance of several subyearling stocks that are common in SRKW critical habitat have increased or remained stable (Atlas et al. 2023, CTC 2024, this study). For example, Fraser River Summer 4_1 returns in 2023 were the largest on record (CTC 2024), continuing a multidecadal increase in abundance. This stock also has a relatively high lipid content and was disproportionately selected by SRKWs, suggesting it is an important prey item; however, this stock is only available in the study area relatively late in the summer due to their northern distribution (CTC 2022, Freshwater et al. 2021, Weitkamp 2010). Conversely, Columbia Fall, Fraser Fall, and Puget Sound individuals are available within the study area over a longer period because of their resident life histories (Freshwater et al. 2021, Shelton et al. 2019, Weitkamp 2010), but typically have lower lipid content and, early in the year, may be smaller (Freshwater and King 2024, Lerner and Hunt 2023, O'Neill et al. 2014). Additionally, many of the populations within these stocks, but not Fraser River Summer 4_1 populations, are heavily enhanced by hatcheries. Efforts to increase prey availability via enhancement should take into account differences among Chinook salmon stocks in marine distributions and SRKW selectivity. For example, increasing the abundance of the ECVI/SOMN may be less effective in the short-term because these individuals are rarely encountered in the western portion of the study area and other outside waters where SRKWs are spending a greater portion of the year (Stewart et al. 2023). Increasing the abundance of the WCVI stock may also be ineffective if SRKWs show negative selection towards this stock despite spatiotemporal co-occurence.

Changes in harvest and enhancement strategies may provide an opportunity to improve SRKW foraging conditions via changes in prey quality, rather than prey abundance. For example, DFO has incorporated maximum size limits in several marine fisheries (DFO 2023*b*). The primary objective of current size limits is to minimize harvest impacts on at-risk CUs; however, these restrictions likely also increase the local abundance of large individuals from other stocks. It may be possible to increase the mean size or lipid content of abundant subyearling Chinook salmon individuals via changes in hatchery practices. Age-at-maturity is both heritable (McKinney et al. 2020) and influenced by environmental factors during freshwater rearing (Larsen et al. 2006). The capacity to increase mean lipid content via changes to enhancement strategies is less clear, but divergent patterns among stocks suggest it is a heritable trait. Nevertheless, the ecological consequences of enhancement are complex and the risks associated with experimental programs should be considered carefully. For example, increasing the abundance of lipid-rich prey species may benefit other salmon predators, increasing competitive pressures on SRKWs and negating any anticipated benefit.

Ultimately multiple, diverse strategies may be more successful than implementing drastic changes in harvest regulations or enhancement alone. Increased prey availability via changes in Chinook salmon size and energy density should be considered alongside reductions in vessel noise to improve SRKW foraging success and habitat restoration in freshwater salmon habitat to improve productivity. Implementing a range of interventions intended to rebuild depleted Chinook salmon populations while simultaneously mitigating non-prey threats and continuing research on the mechanisms of declines in Chinook salmon productivity is consistent with previous recommendations (Hilborn et al. 2012).

4.7. LIMITATIONS AND FUTURE RESEARCH DIRECTIONS

Although we incorporated multiple datasets to estimate variability in SRKW prey preference among Chinook salmon, our study had several limitations. We were forced to make the assumption that fisheries-dependent samples reflected Chinook salmon available to SRKW because there are no fisheries-independent data available to quantify stock composition in marine areas. Gear selectivity or fisher behaviour may cause fisheries-dependent data to differ from the underlying population and these biases may vary among groups of harvesters (i.e., fleets). Despite including at least three potential fleets, we were unable to estimate these effects statistically.

Management interventions intended to minimize harvest impacts on at-risk Chinook salmon CUs may amplify biases associated with fisheries-dependent data. Domestic restrictions on harvest based on size and mark status, as well as time-area closures, have varied seasonally, spatially, and interannually, but have been present in some portion of Canadian critical habitat since 2008 (Dobson et al. 2020 provide a detailed summary of actions prior to 2019, while recent closures are summarized in DFO 2023*b*). Generally restrictions were most severe in statistical areas east of 20-3 (approximately central Juan de Fuca Strait), prior to August 1, and from 2019 onwards. Data collected in Nitinat, as well as in Swiftsure Bank and Port Renfrew strata prior to 2019 or after August 1 since 2019, are relatively unbiased because only standard size and bag limits were in place (Figure A.3). Additionally, samples from released fish were relatively common (25-50% of samples per event since 2018) in locations from Haro Strait to the southern Gulf Islands, which will reduce bias in the southern Gulf Islands strata. Thus predicted composition estimates are most likely to be biased in locations between Victoria and Sooke, where management interventions were present during May and June since before 2014 and sampling of released fish was rare.

The combination of mark-selective fisheries with maximum size limits and limited sampling of released fish between Sooke and Victoria may have reduced the relative proportion of individuals from the largest size bins and increased the apparent abundance of Puget Sound fish, which are both abundant and have a high mark rate. Yet without additional fisheries-independent sampling or complex run reconstruction models it is not possible to quantify the bias of stock and size composition estimates in these areas. Although composition estimates based on fisheries samples may be biased by changes in management regime, these effects did not impact the results of our selectivity analysis. Nearly all SRKW prey remains samples from the current sampling period were collected in locations west of area 20-3 and from July onward—i.e., the simulation analysis compared prey remains to model outputs that were parameterized with fisheries-dependent data collected during times and locations with negligible additional management measures. Excluding the small number of prey remains samples that were collected when recreational fisheries were closed or size limits were in place did not impact the results of the selectivity analysis (Appendix D).

Prey remains were also only available for a single species, during summer months, and over a relatively small portion of the SRKW range. Our results provide no information on SRKW selectivity in locations or periods where prey remains were not collected. Columbia-origin Chinook salmon stocks may be favored in locations such as coastal Washington (Shelton et al. 2019) or Canadian stocks with later run-timing or greater relative abundance (e.g., Fraser River Fall) may be preferred in the southern Strait of Georgia (Freshwater et al. 2021). Indeed Columbia River Chinook salmon are commonly observed in SRKW prey remains collected from coastal Washington, particularly overwinter and in early spring (Hanson et al. 2021). Ideally, similar tests for selectivity could be replicated in other locations and seasons. There is also considerable

evidence that other prey species may be important components of the SRKW diet outside summer months (Hanson et al. 2021, Van Cise et al. 2024). Research should be expanded beyond Chinook salmon to better understand prey availability during seasonal periods when SRKW may be most prey limited. Such research is particularly critical given recently observed declines in southern BC chum salmon abundance, another prey species dominant in SRKW diets (Hanson et al. 2021, Van Cise et al. 2024).

Variability among Chinook salmon stocks and size classes within SRKW diets is a function of both selectivity and local abundance. Due to stock-specific behaviours or distributions, local abundance within SRKW foraging habitat may or may not be highly correlated with a stock's absolute abundance. Since we were unable to evaluate local abundance and selectivity throughout all SRKW foraging habitats we cannot provide an assessment of each Chinook salmon stock's absolute importance as SRKW prey. Rather, our results emphasize that the prey field available to SRKW varies over small spatiotemporal scales and our model provides a tool to quantify stock-specific *relative* abundance at specific times and locations. Additional research is necessary to integrate information on stock-specific abundance and fine-scale distributions, as well as resident killer whale habitat use. Future research focused on identifying the mechanisms contributing to divergent dynamics among Chinook salmon stocks (e.g., Fraser River Spring and Summer 5_2 vs. Summer 4_1) may also be valuable to informing stock rebuilding efforts.

We had insufficient statistical power to adequately model variability in SRKW prey remains and were therefore unable to evaluate changes in diet between the early and current sampling period. Similarly, a lack of genetic sampling in fisheries prior to 2014 prevented an analysis of long-term trends in stock composition. In the absence of these data, readily available stock-specific return abundance (i.e., catch plus escapement) could be used as a proxy for long-term trends in Chinook salmon abundance (e.g., Atlas et al. 2023), as well as abundance in foraging areas (e.g., Nelson et al. 2024, Ward et al. 2009*b*). We note that there is not evidence of a widespread, uniform decline in aggregate Chinook salmon terminal abundance within the study area, but instead divergent patterns among and within stocks (Atlas et al. 2023, CTC 2024, this study).

Terminal abundance data provide an index of minimum abundance. They cannot account for escapement to every system within a region, but more importantly they do not account for marine harvest or the abundance of immature individuals. Changes in management regime are less likely to impact linkages between terminal abundance and prey availability because large-scale commercial fisheries historically occurred seaward of Canadian SRKW critical habitat (i.e., west coast Vancouver Island, northern British Columbia, and southeast Alaska). Terminal abundance estimates also fail to account for stock-specific spatiotemporal distributions that impact their availability as prey to SRKW. We suggest that future analyses focus on the stocks that are most likely to serve as prey, based on spatiotemporal overlap with SRKW foraging areas, rather than large multi-stock aggregates. Analyses may be improved by scaling abundance estimates by the proportion of a stock that migrates through SRKW habitat and its residence time. Even if these analytical improvements are made, however, we urge researchers to be cautious when interpreting statistical relationships between Chinook salmon abundance and SRKW dynamics as strictly mechanistic, particularly given the relatively short time series of salmon abundance that are available.

4.8. CONCLUSIONS

We used fisheries-dependent data and samples from SRKW prey remains to better understand seasonal and spatial variability in Chinook salmon abundance in the context of prey available to

SRKWs. Sufficient data were available to estimate mean stock and size composition throughout the study area (Swiftsure Bank to the southern Gulf Islands) between May and October (June and September in western areas). Our results emphasize that SRKWs encounter a diverse range of Chinook salmon stocks. Adequate prey availability likely depends on access to multiple stocks with distinct spawning distributions and life histories. It may be possible to improve the efficacy of management measures by focusing interventions on Chinook salmon stocks that are abundant within SRKW foraging habitats during periods of energetic stress, rather than those that are abundant throughout southern British Columbia waters as a whole. SRKWs show evidence of size- and lipid-selectivity, and appear to be in particularly poor physical condition early in the year. Thus we suggest that management actions intended to increase prey availability should prioritize increasing the abundance of large, lipid rich prey, particularly during the spring and early summer, and we caution against using coarse, multistock indices of abundance to draw inference on prey availability. Finally, we note that our conclusions reflect current ecological processes, which may be impacted by changes in SRKW or Chinook salmon abundance and behaviour, particularly given ongoing climate change.

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APPENDIX A. SUPPLEMENTARY FIGURES

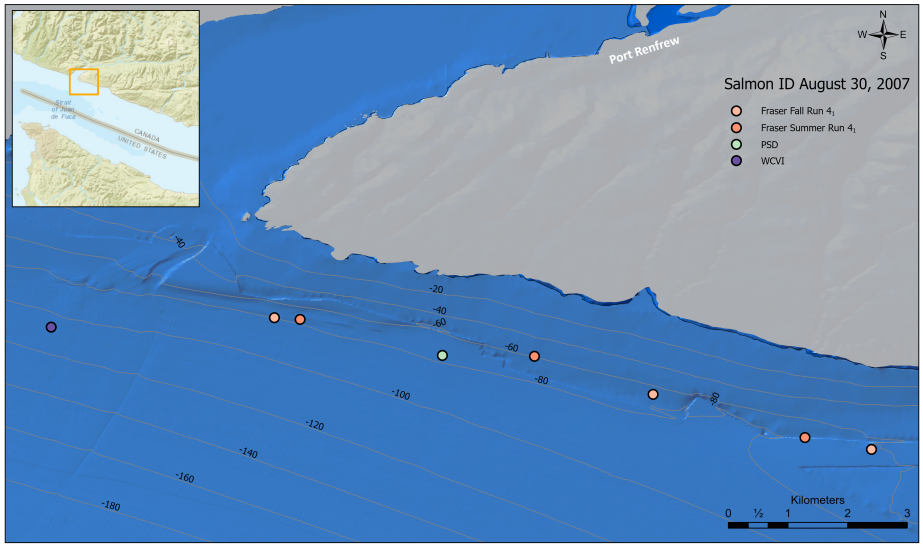

Figure A.1. Locations and stock identity (highest probability for a given sample) of SRKW prey remains collected August 30, 2007.

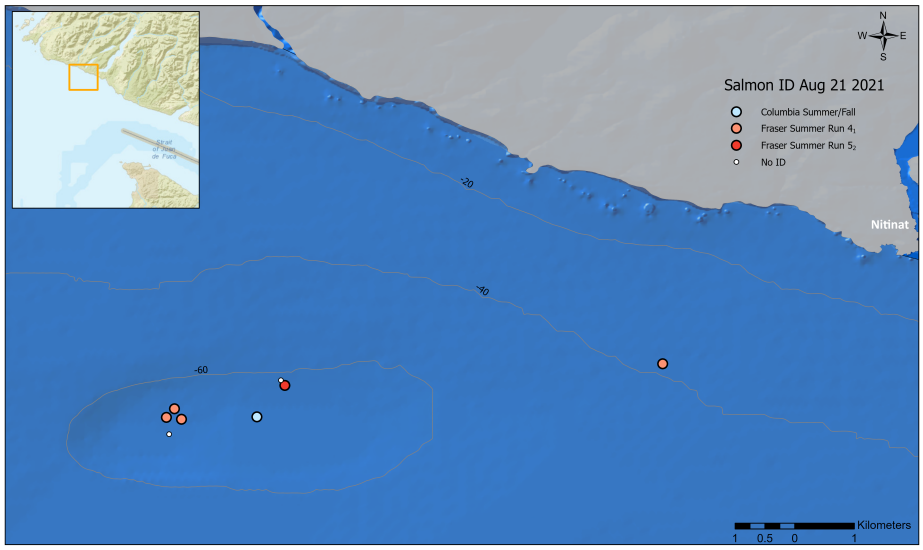

Figure A.2. Locations and stock identity (highest probability for a given sample) of SRKW prey remains collected August 21, 2017.

Figure A.3. Temporal distribution of Chinook salmon stock composition samples originating from recreational fisheries between May and October, and associated additional management measures (colours). Strata (panels) correspond to spatial domains in Figure 2. Samples collected during non-retention were either from Avid Anglers samples of released fish or scientific Reference Fisheries. Note that this figure is not intended to precisely capture management actions. Size limits vary among and within strata and may include both minimum and maximum size limits. For detailed information on specific interventions consult Dobson et al. 2020 for years prior to 2019 and annual IFMPs (e.g., DFO 2023). Point size scaled to number of individual samples collected within a given fishing location, week, and year. Points have been jittered to maximize visibility.

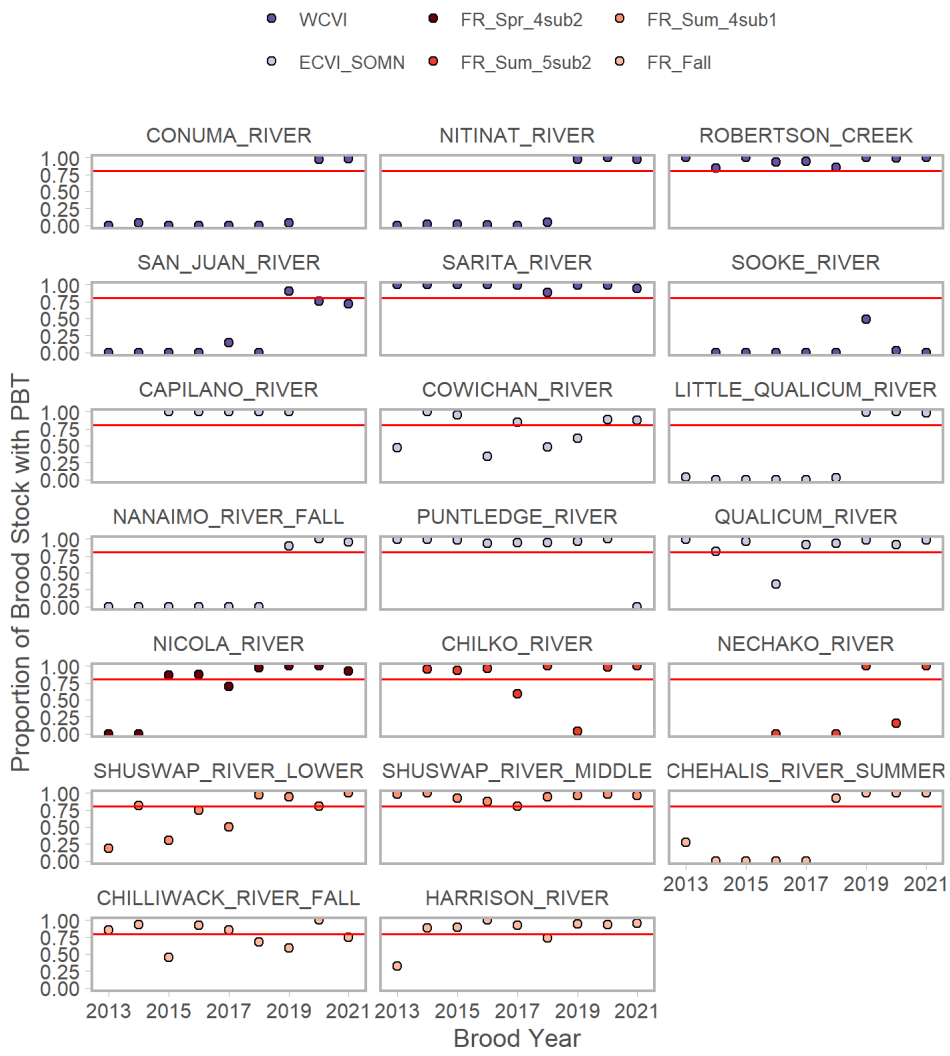

Figure A.4. The proportion of hatchery Chinook salmon brood stock, by brood year, incorporated into the PBT database. Horizontal red line represents threshold tagging rate below which individuals identified with GSI were assigned an unknown origin. Only major enhancement facilities (average annual releases greater than 140,000) with migration routes near the study area are shown. Nechako and Chilko have mean annual release sizes less than 140,000, but are shown because both stocks were relatively abundant in recreational fisheries. Note that brood years precede return years by at least two years.

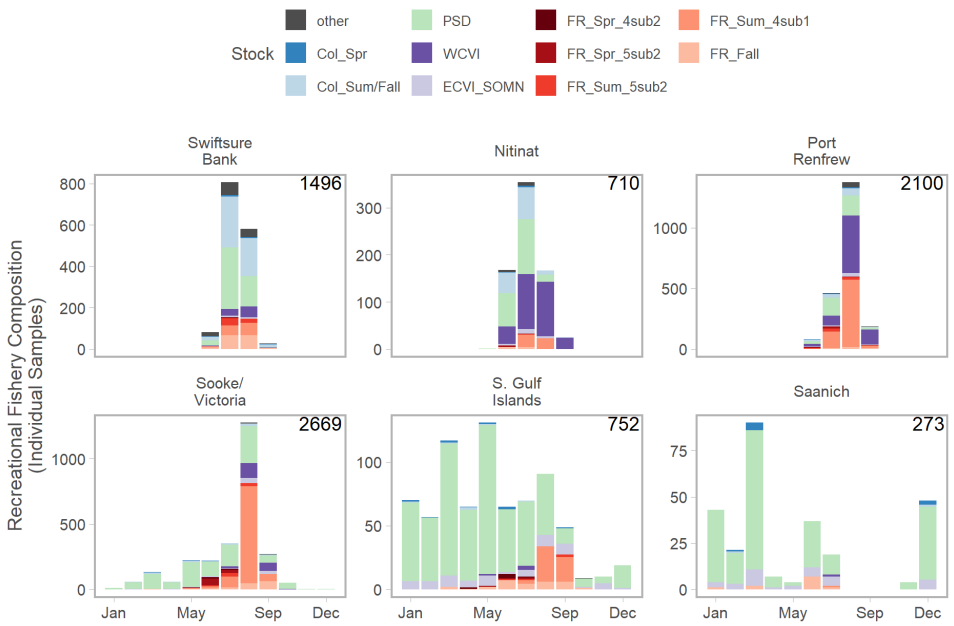

Figure A.5. Monthly stock composition of recreational Chinook salmon fishery samples during all months. Strata (panels) correspond to spatial domains in Figure 2. Y-axis represents the number of samples collected in a given month and spatial strata. Numerals in upper right corner of each panel represent the total sample size in each strata.

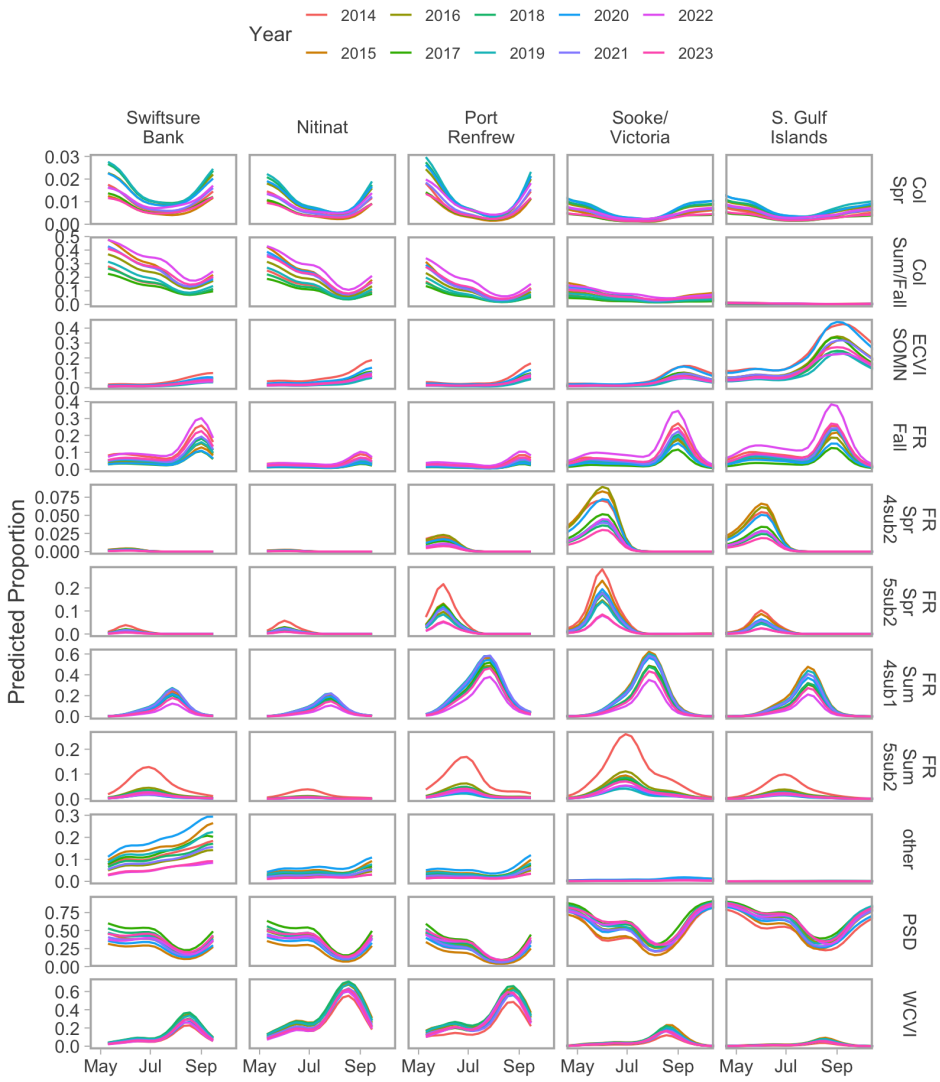

Figure A.6. Predicted year-specific mean stock composition. Strata (panels) correspond to spatial domains in Figure 2. Confidence intervals not shown to improve readability.

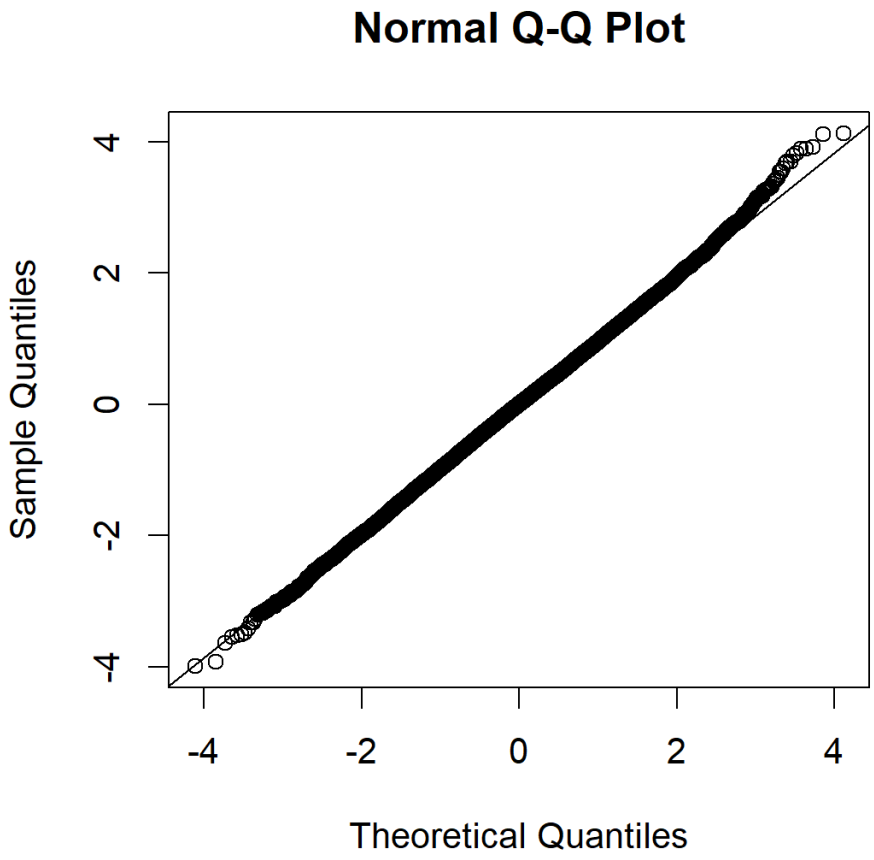

Figure A.7. Model residuals calculated using MCMC draws from posterior distribution of predictions with fixed effects at maximum likelihood estimates and random effects (i.e., residual variance) sampled from Tweedie distribution.

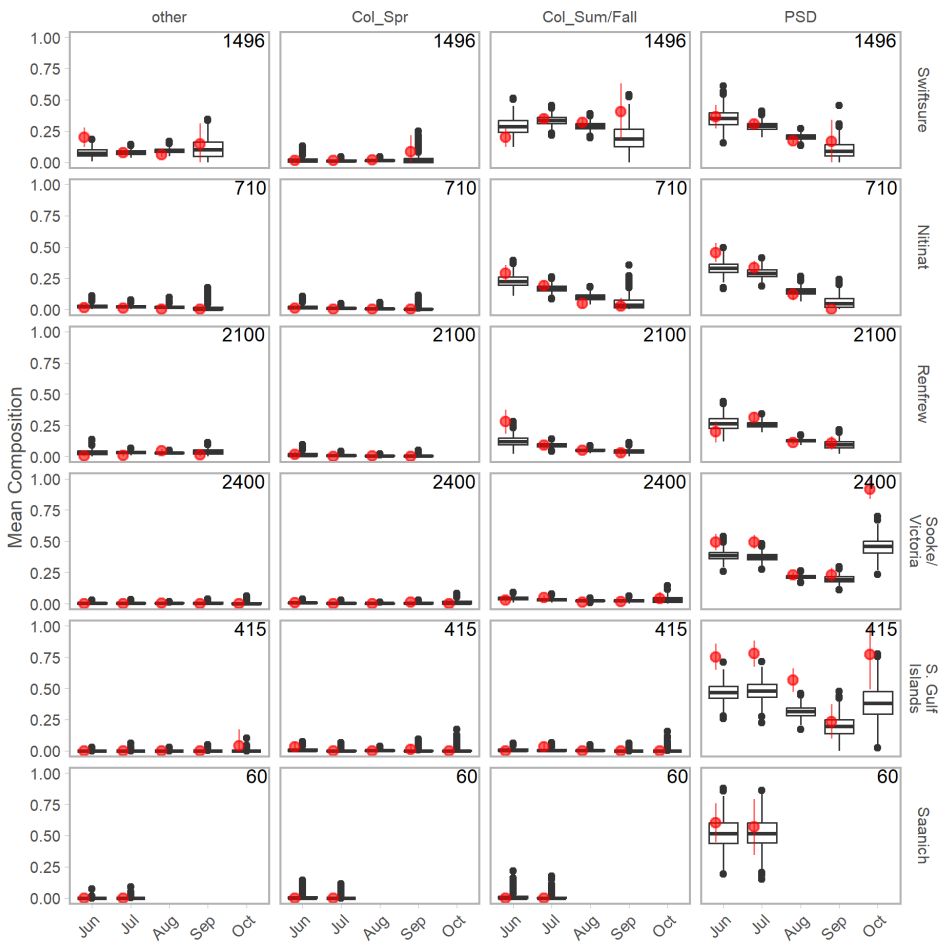

Figure A.8. Model simulated (box plots) and observed (red points) mean stock composition for "other", Columbia Spring, Columbia Summer/Fall, and Puget Sound stocks. Simulations represent 500 draws from the estimated multivariate Tweedie model, including residual variance, fit to the original dataset. Red whiskers represent approximate 95% confidence intervals associated with observed sample. Mean stock composition calculated for each strata and month. Strata (panels) correspond to spatial domains in Figure 2.

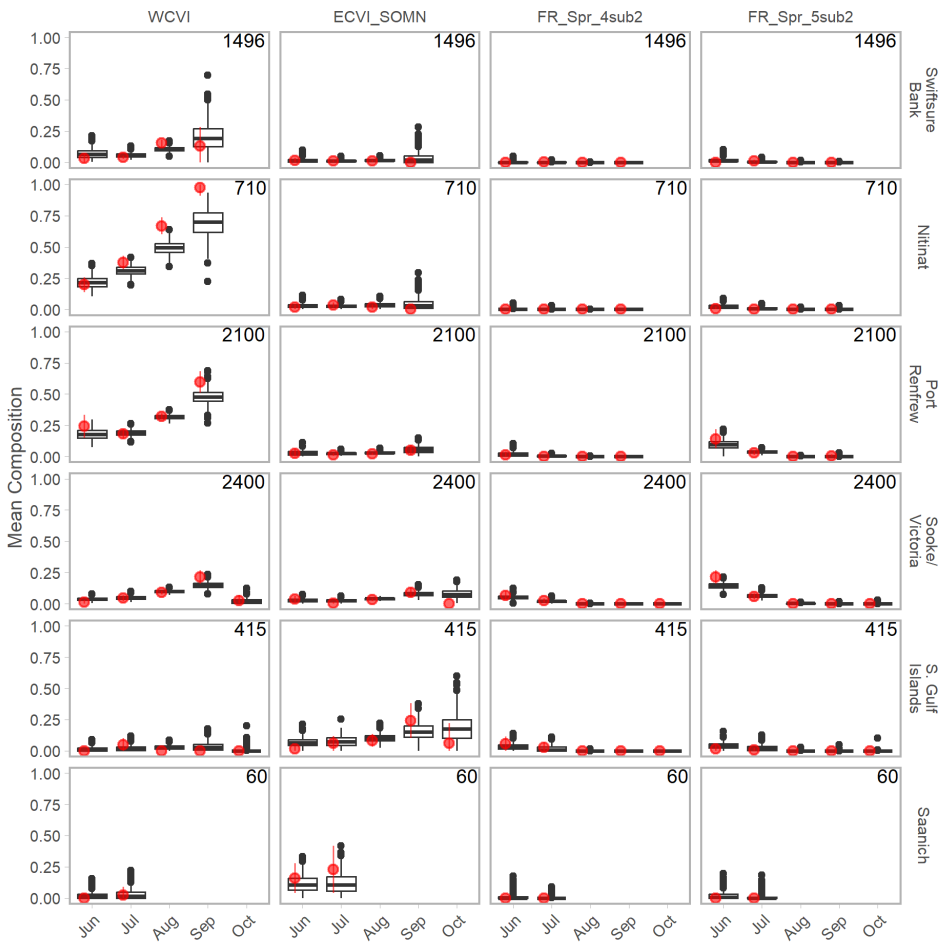

Figure A.9. Model simulated (box plots) and observed (red points) mean stock composition for West Coast Vancouver Island, East Coast Vancouver Island/southern mainland, Fraser Spring 4_2, and Fraser Spring 5_2 stocks. Simulations represent 500 draws from the estimated multivariate Tweedie model, including residual variance, fit to the original dataset. Red whiskers represent approximate 95% confidence intervals associated with observed sample. Mean stock composition calculated for each strata and month. Strata (panels) correspond to spatial domains in Figure 2.

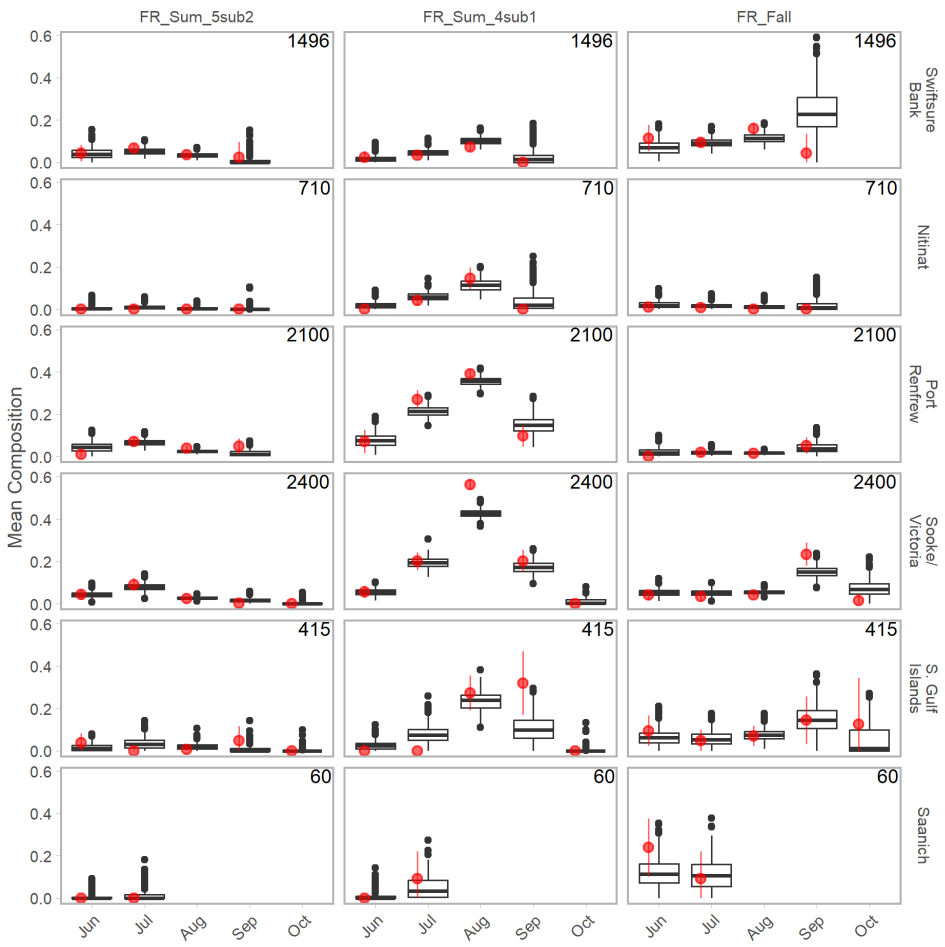

Figure A.10. Model simulated (box plots) and observed (red points) mean stock composition for Fraser Summer 5_2, Fraser Summer 4_1, and Fraser Fall stocks. Simulations represent 500 draws from the estimated multivariate Tweedie model, including residual variance, fit to the original dataset. Red whiskers represent approximate 95% confidence intervals associated with observed sample. Mean stock composition calculated for each strata and month. Strata (panels) correspond to spatial domains in Figure 2.

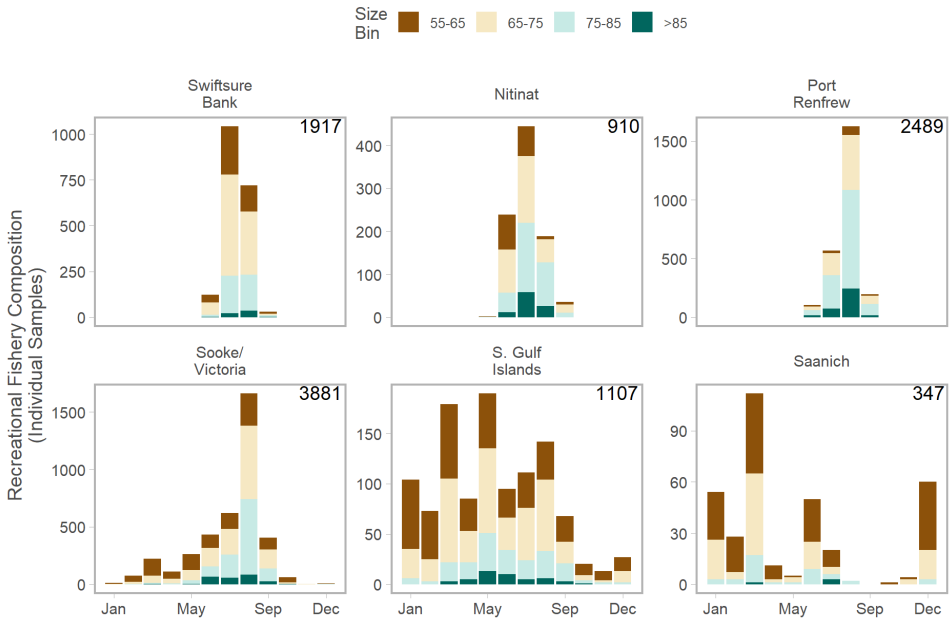

Figure A.11. Monthly size composition of recreational Chinook salmon fishery samples during all months. Strata (panels) correspond to spatial domains in Figure 2. Y-axis represents the number of samples collected in a given month and spatial strata (note scale differs among strata). Numerals in upper right corner of each panel represent the total sample size in each strata.

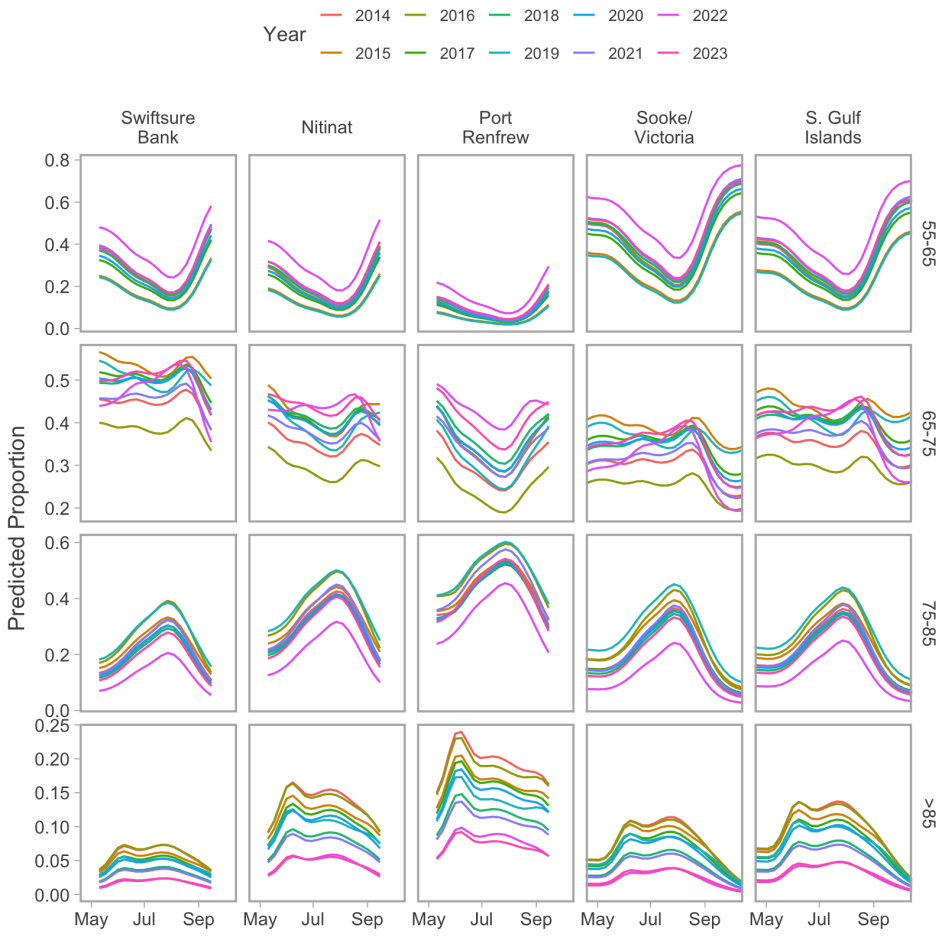

Figure A.12. Predicted year-specific mean size composition. Strata (panels) correspond to spatial domains in Figure 2. Confidence intervals not shown to improve readability.

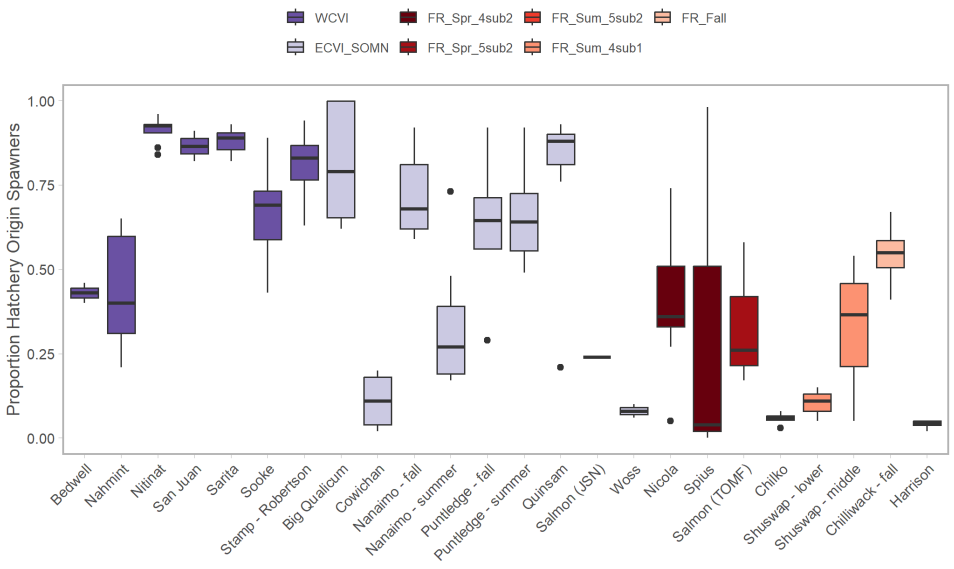

Figure A.13. The estimated proportion of hatchery-origin spawners for a subset of Canadian Chinook salmon populations. Box plots represent variability among years (2014-2022). Colors represent Canadian-origin stocks.

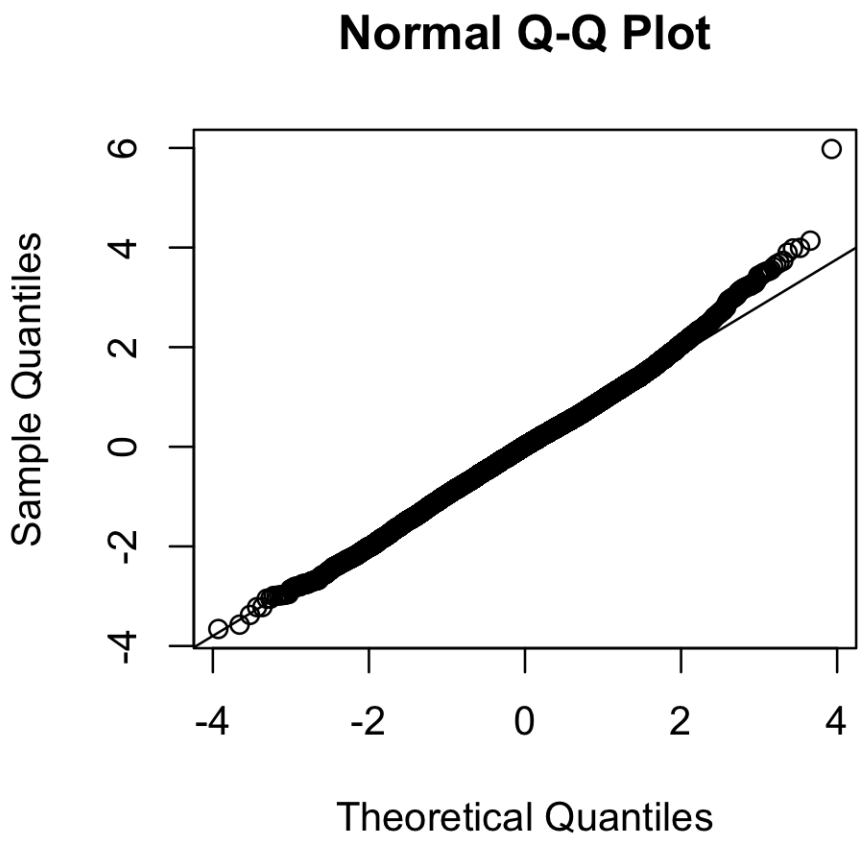

Figure A.14. Quantile-quantile plot of size composition model residuals calculated using MCMC draws from posterior distribution of predictions with fixed effects fixed at maximum likelihood estimates and random effects (i.e., residual variance) sampled from negative binomial distribution.

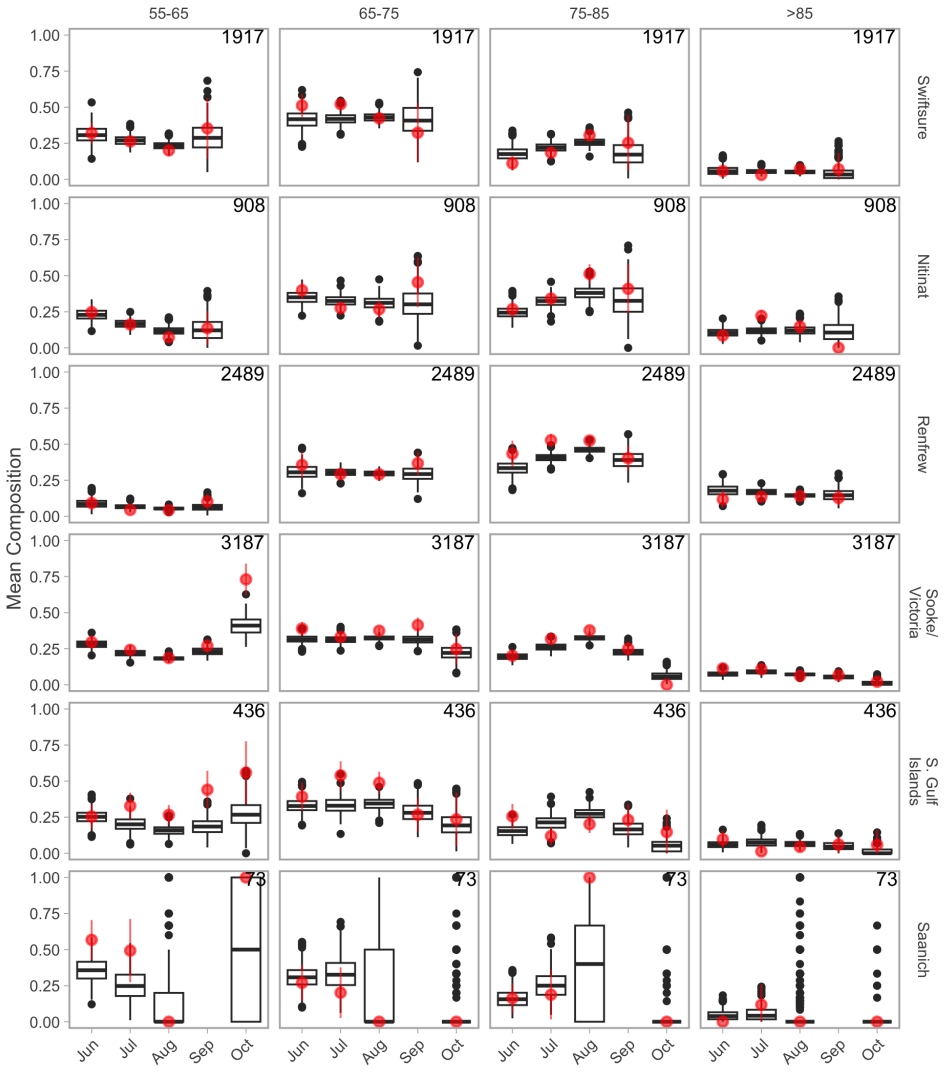

Figure A.15. Model simulated (box plots) and observed (red points) mean stock composition. Simulations represent 500 draws from the estimated Tweedie model, including residual variance, fit to the original dataset. Red whiskers represent approximate 95% confidence intervals associated with observed sample. Mean stock composition calculated for each strata and month. Strata (panels) correspond to spatial domains in Figure 2.

APPENDIX B. ESTIMATING SIZE OF PREY REMAINS

We combined estimates of age assignment uncertainty and stock-specific size-at-age to convert marine age estimates for SRKW prey remains into estimates of the probability that a given sample belonged to one of four size bins.

B.1. AGE ASSIGNMENT UNCERTAINTY

SRKW prey remains were aged using scale annuli by technicians at the Fish Ageing Laboratory at the Pacific Biological Station's Sclerochronology Lab (Fisheries and Oceans Canada, Nanaimo, British Columbia, Canada). Age assignments based on scales are commonly used in Pacific salmon stock assessments and accuracy is typically high (McNicol and MacLellan 2010); however, these estimates may deviate from the true age resulting in error. We first estimated the magnitude and direction (i.e., over- vs. underestimate) of ageing error using data from Chinook salmon with both an age estimated from scale readings, as well as a known age from coded wire tags or parentage based tags. We then fit a hierarchical model to estimate the ageing error associated with a sample collected from SRKW prey remains.

Estimated and true age data were available from 16,528 Chinook salmon. These data originated from the recreational fishery dataset presented in the main text, as well as data from Fraser and Interior Area Stock Assessment, which collected samples as part of freshwater test fisheries and escapement sampling. Although samples were available from each of the stocks included in the main text, stock-specific sample sizes ranged widely (e.g., two samples for Columbia River Spring, 4,508 for Fraser River Fall). We did not account for stock assignment uncertainty in this analysis. Each sample was assigned to one of three bias categories: zero (estimated and true ages were the same), underestimate (true age greater than estimated age), or overestimate (true age less than estimated age). We excluded 48 samples where the difference between true and estimated ages was greater than one year.

The directionality of errors differed among estimated ages–fish estimated to be greater than age four were more likely to be overestimated, while those estimated to be younger than age four were more likely to be underestimated (Figure B.1). Accuracy was also typically highest for the dominant age classes in a stock (Figure B.1).

To generate estimates of ageing error for SRKW prey remains, we fit a hierarchical multinomial model in which the three bias categories (zero, under, or over) were the response variable, estimated age was a fixed effect, and stock identity was a random intercept. This structure allowed us to generate age- and stock-specific error rates, while leveraging data-rich stocks to inform data-limited stocks. We fit the model in Stan via the brms package (Bürkner 2017), using weakly informative priors. We used the fitted model to convert the estimated age associated with each SRKW prey sample to a vector of total age a_t assignment probabilities $\boldsymbol{q}_{\boldsymbol{a_t}}$, which incorporated age- and stock-specific error rates. For example, a sample identified as originating from a Fraser Fall individual with an estimated total age of five years might result in a 50% probability of being age-4 and a 50% probability of being age-5.

B.2. SIZE-AT-AGE ESTIMATES

To estimate prey size from scale samples, we used a statistical model to predict size-at-age using data from the recreational Chinook salmon fishery. Here we assumed a stock assignment

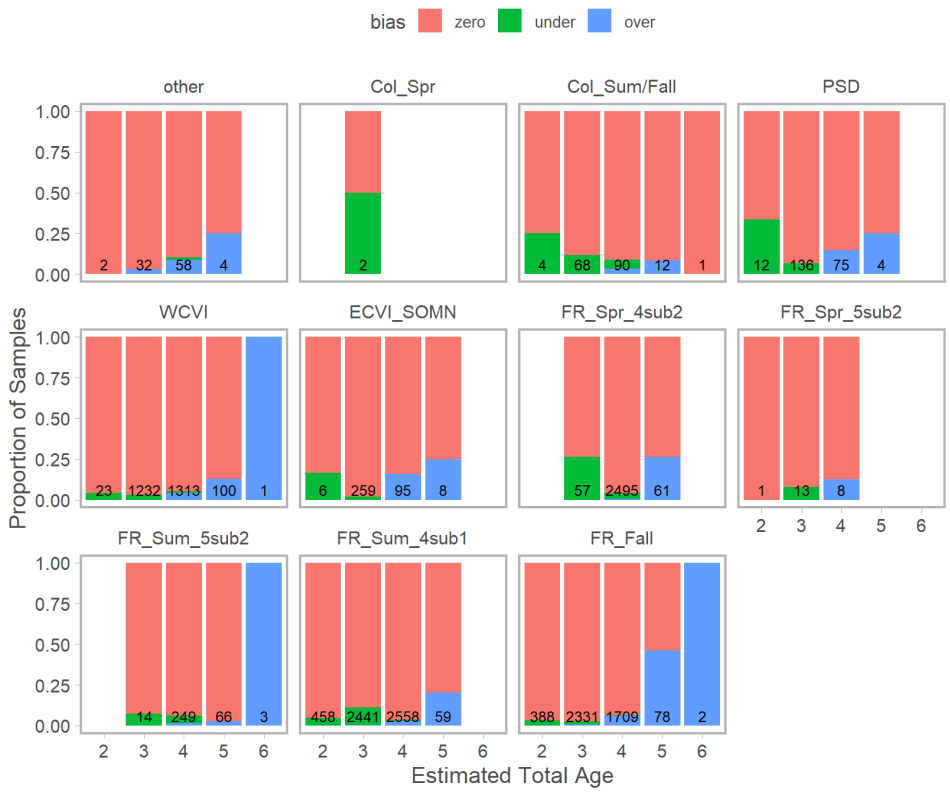

Figure B.1. Bias in estimated total age among Chinook salmon stocks. Numerals represent the number of samples in a given age class and stock.

probability greater than 75% was accurate and excluded samples below this threshold. Marine age, body size, and stock identity estimates were available for 7,815 Chinook salmon larger than 550 mm fork length. We estimated size b for stock s using the following generalized additive model:

$$b_s \sim \text{Normal}\left(\mu_{b_s}, \sigma^2\right), \tag{1B}$$

$$\mu_{b_s} = \alpha_s + \alpha_a + f_w w + f_{w_s} w + f_{w_a} w + \alpha_y \tag{2B}$$

Where α_a represents an intercept for marine age a and α_s represents an intercept for each stock. We represented seasonal changes in body size with f_w, a Gaussian process smooth function for sampling week w. We also allowed seasonal variability to differ among among stocks and marine age classes, using hierarchical smooths f_{w_s} and f_{w_a}. Finally, we included a random intercept α_y representing year-specific changes in mean size. We modeled α_y assuming a hyperdistribution with mean zero and standard deviation σ_y. Note that stock groupings used in the size-at-age model were more finely resolved than those used in the stock composition analyses to increase the precision of predictions.

We used the fitted model to visualize seasonal patterns in stock-specific size-at-age and predict the mean size of each SRKW prey sample that had a viable age estimate based on the associated stock identity and sampling week. We did not generate year-specific predictions (i.e., integrated out α_y) given that many samples were collected prior to recreational fishery sampling.

Chinook salmon stocks captured in the study area differed in marine age, but generally marine age-2 and age-3 individuals were most common (Figure B.2). Note that these observations will under-represent marine age-1 and -2 individuals (particularly for subyearling life histories) because they exclude individuals smaller than 550 mm fork length to remain consistent with the rest of the analysis.

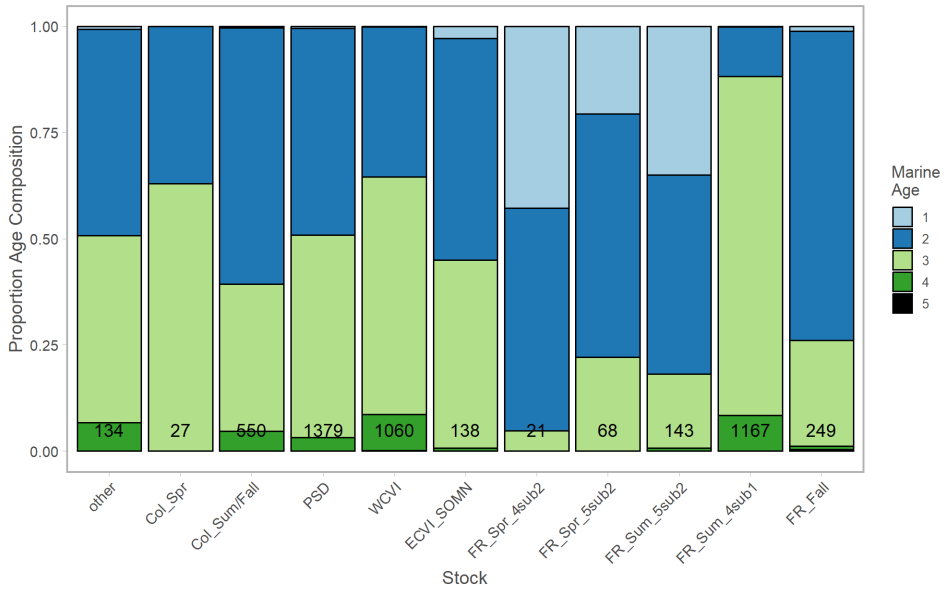

Figure B.2. Observed marine age of Chinook salmon from southern BC recreational fisheries.

Older marine ages were larger than younger marine ages and stocks varied in size-at-age, with yearling stocks typically larger at marine age-2 than subyearling stocks (Figure B.3). Chinook salmon showed evidence of changes in body size over the summer; however, these trends differed among stocks and among marine age classes. The model accurately captured variability in size within age classes, which resulted in overlapping size distributions (Figure B.4).

We used the fitted model to generate a posterior distribution of 1000 samples of body size for each combination of stock, marine age, and month observed in the SRKW prey remains.

B.3. PROPAGATING UNCERTAINTY TO SRKW PREY REMAINS SIZE ESTIMATES

We used a multi-step process to identify a vector of probabilities that a given SRKW prey remains sample belonged to one of the four size bins b'. First, we converted the vector of total age probabilities $\boldsymbol{q_{a_t}}$ to a vector of marine age probabilities $\boldsymbol{q_a}$, based on the marine age of the sample when an estimate was available or based on a stock's dominant life history otherwise. Second, for each sample we drew from the previously described posterior distributions of stock-, marine age-, and month-specific body size estimates proportionally to $\boldsymbol{q_a}$. Assuming the previously described example was collected in June and belonged to a Fraser Fall individual with a 50% age-4 probability of being age-4 and a 50% probability of being age-5, then we would draw 500 samples from the June Fraser Fall age-4 size distribution and 500 samples from the June Fraser Fall age-5 size distribution (e.g., Figures B.3, B.4). Third, we converted each size sample to a size bin b' and calculated the proportion of the 1000 samples belonging to each bin, creating a vector of size bin probabilities $q_{b'}$ for each sample.

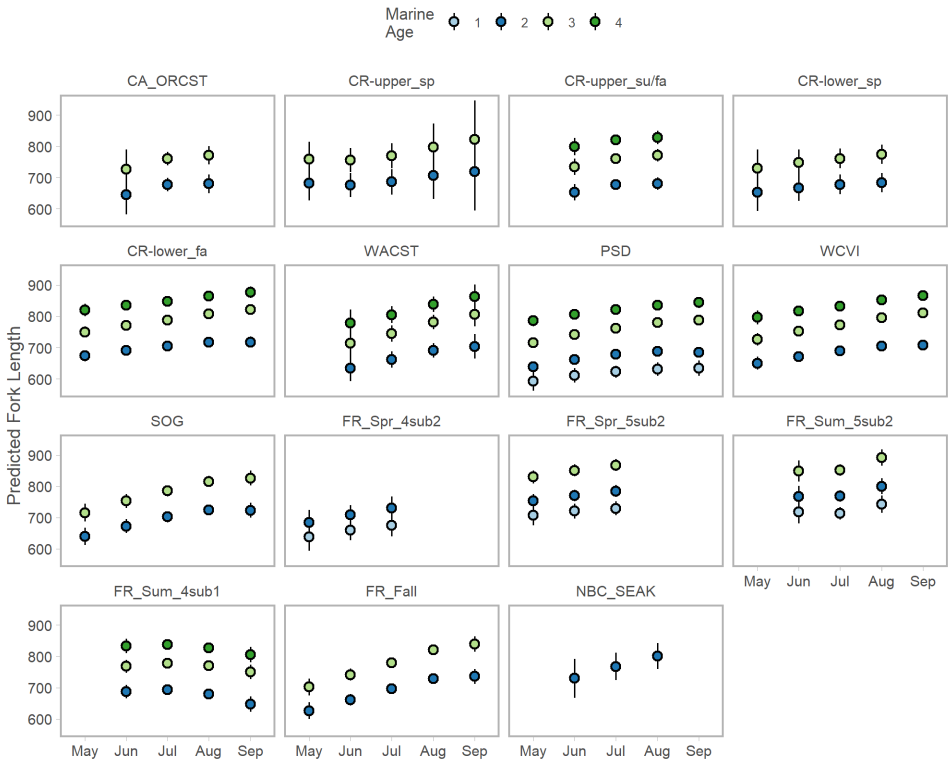

Figure B.3. Model predicted size-at-age. Points represent means and whiskers 95% confidence intervals. Predictions are only shown for months and marine ages where at least five individuals from the relevant stock were available to parameterize the model.

To ensure this analysis was tractable we did not propagate stock assignment uncertainty. Instead we used the maximum stock assignment probability for each individual sample to generate $q_{b'}$. We believe this assumption is unlikely to strongly impact our results given: similar age biases among stocks, broadly overlapping size-at-age distributions among stocks (Figure B.4), prey samples with an assignment probability less than 60% were excluded, and that 90% of the included samples had an assignment probability greater than 80%.

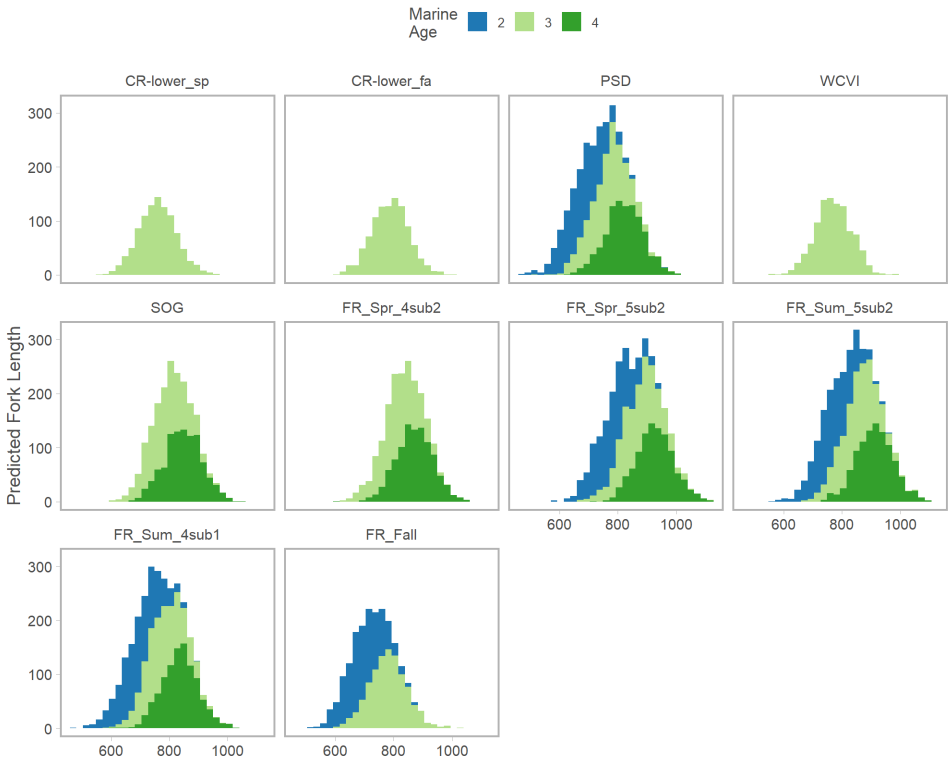

Figure B.4. Model predicted size-at-age distributions for July. Distributions have the same means as Figure B.3, but incorporate residual variability around the mean. Only age and stock combinations observed in SRKW prey remains are shown.

APPENDIX C. TERMINAL ABUNDANCE

We collated data on terminal abundance for American stocks from the Pacific Fishery Management Council historical dataset of escapements to inland fisheries and spawning areas (PFMC 2024). Terminal abundance data for Canadian stocks originated from DFO stock assessment area offices (Table C.1).

Table C.1. Terminal abundance definitions and sources by stock.

Stock	Data Included	Source
Washington and Oregon Coastal[1]	Terminal catch plus escapement[2]	PFMC (2024)
Columbia River Summer/Fall	In-river catch plus escapement	PFMC (2024)
West Coast Vancouver Island	Catch inside surfline (i.e., PFMAs 23-27) and in-river plus escapement	DFO South Coast Stock Assessment; Nick Brown, pers. comm.
East Coast Vancouver Island/Southern Mainland Inlets	Escapement	DFO South Coast Stock Assessment; Kevin Pellett, pers. comm.
Puget Sound	Escapement plus terminal catch	PFMC (2024)
Fraser River Spring 42	In-river catch plus escapement	DFO 2024; Brittany Jenewein, pers. comm.
Fraser River Spring 52	In-river catch plus escapement	DFO 2024; Brittany Jenewein, pers. comm.
Fraser River Summer 52	In-river catch plus escapement	DFO 2024; Brittany Jenewein, pers. comm.
Fraser River Summer 41	In-river catch plus escapement	DFO 2024; Brittany Jenewein, pers. comm.
Fraser River Fall	In-river catch plus escapement	DFO 2024; Brittany Jenewein, pers. comm.

[1] Washington and Oregon Coastal stocks grouped with “Other” stock in main text.
[2] Escapement includes natural spawners, brood stock capture, and swim-ins to hatchery facilities for all stocks.

Stock-level terminal abundance estimates are based on catch and escapement monitored at indicator systems, which are then summed. We excluded indicator systems with incomplete monitoring between 1983 and 2022 to avoid temporal bias due to changes in sampling. Thus terminal abundance estimates should be interpreted as minimum estimates of abundance, particularly given that in some stocks only a subset of reaches are monitored. For Washington Coastal and Puget Sound stocks 2023 data were unavailable and were interpolated using mean values 2019-2022 (cycle line average). For East Coast Vancouver Island and Southern Mainland Inlets, stock-level data were generated by interpolating estimates for sparsely observed indicator systems based on the mean proportional abundance of regularly monitored systems (e.g., Cowichan River) in years where all systems were observed. Finally, we excluded terminal abundance estimates collected prior to 1982 due to relatively few complete time series.

APPENDIX D. SENSITIVITY ANALYSES

D.1. SIZE SELECTIVITY

We accounted for SRKW size selectivity by excluding samples from the recreational fishery that were smaller than 75 cm fork length (>70% of diet samples were estimated to be greater than this size) and refitting the model presented in the main text (Equation 1). Note that the size composition simulation presented in the main text is explicitly testing for size selectivity. The analysis presented here was only used to evaluate the interaction between size and stock selectivity.

We generated predictions (marginal effects) of seasonal stock composition across strata and qualitatively compared those predictions to the model predictions from the main text. We also evaluated the effect of the sensitivity analysis on the stock selectivity simulation, using a model fit only to samples collected from fish larger than 75 cm fork length to generate alternative vectors of mean stock composition ($\pi_{\hat{s_{size}}}$).

We note that this sensitivity analysis is not a comprehensive evaluation of sampling bias. For example, the behaviour of the recreational fleet was impacted by a range of management measures that change seasonally, spatially, and among years (DFO 2023*b*, Dobson et al. 2020). Similarly, prey remains may be more likely to be collected from Chinook salmon stocks with particular behaviours. While it was not possible to account for these confounds statistically, we explore their potential impacts in the Discussion of the main text.

Generally seasonal patterns in stock composition were similar regardless of whether models were fit to the full dataset (main text) or one constrained to only large individuals. However, there were subtle differences for specific stocks, strata, and time periods. For example, the 'Other', Puget Sound, and ECVI/SOMN stocks were relatively less abundant in specific strata when smaller individuals were excluded (Figures D.1, D.2). Conversely, the Fraser River stocks, excluding Spring 4_2 individuals, were typically more abundant when smaller individuals were excluded (Figure D.2).

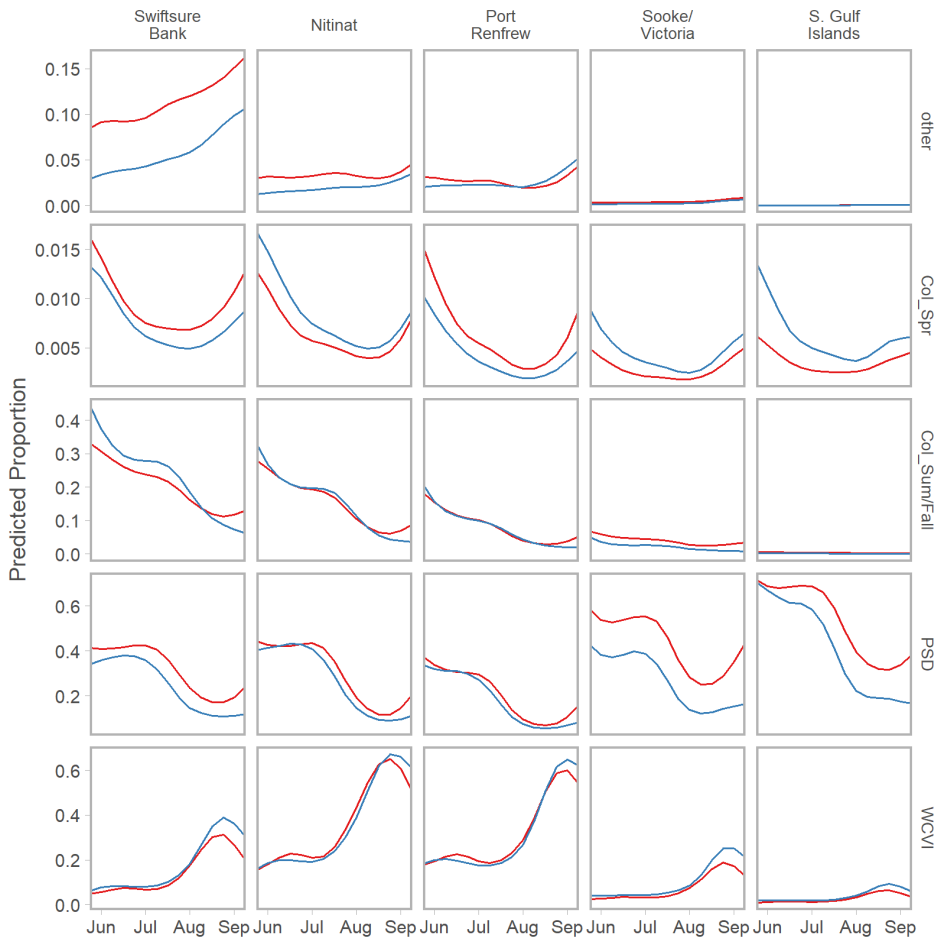

Figure D.1. Seasonal predictions of stock-specific abundance for other, Columbia Spring, Columbia Summer/Fall, Puget Sound, and West Coast Vancouver Island stocks. Predictions are based on the standard model presented in the main text (red), as well as a model fit only to data from individuals larger than 75 cm (blue). Predictions represent mean estimates and confidence intervals are not shown to improve readability. Note differences in y-axis scale among stocks.

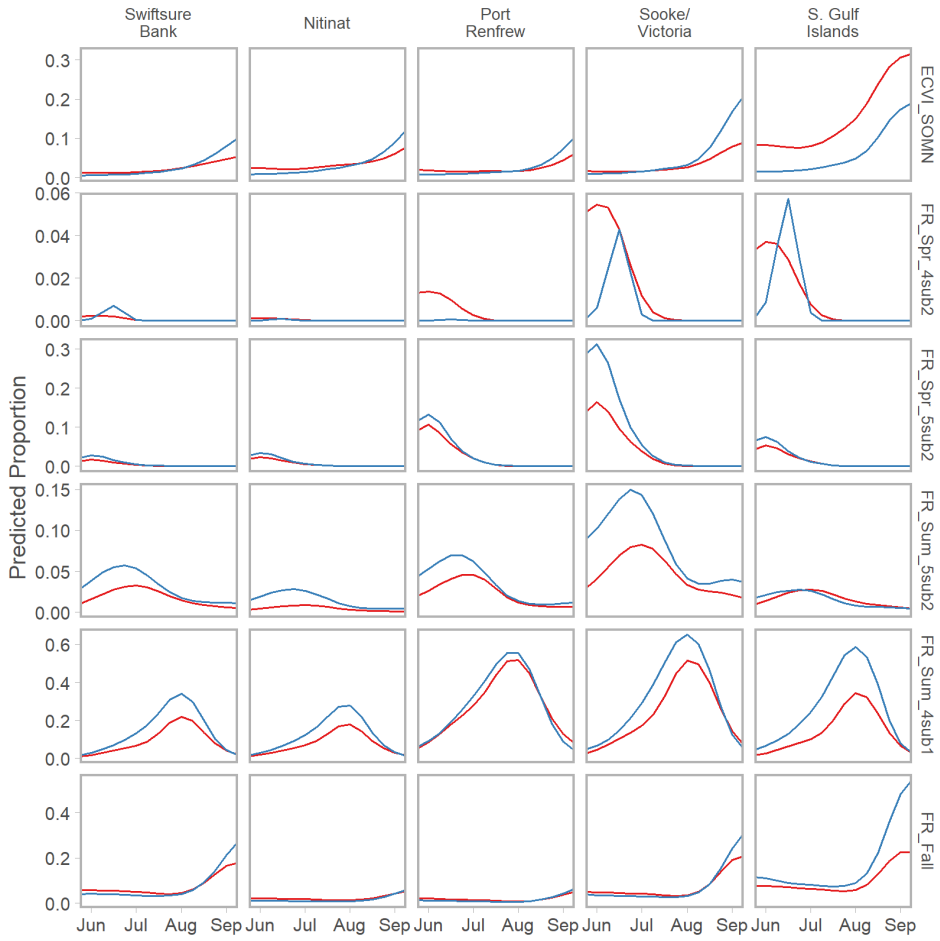

Figure D.2. Seasonal predictions of stock-specific abundance for ECVI/SOMN and Fraser River stocks. Predictions are based on the standard model presented in the main text (red), as well as a model fit only to data from individuals larger than 75 cm (blue). Predictions represent mean estimates and confidence intervals are not shown to improve readability. Note differences in y-axis scale among stocks.

The large scenario model's simulated composition was slightly more consistent with the observed prey remains (Figure D.3). For example, the difference in the proportional abundance of Puget Sound fish shrank. These patterns suggest size selectivity by SRKW did contribute to differences in stock composition between model predictions and observed samples. Nevertheless, these differences were modest and there was still strong evidence of over-representation for Fraser River Summer 4_1, Summer 5_2, and Spring 5_2 stocks, as well as under-representation of the WCVI, Columbia River Summer/Fall, and 'Other' stocks (Figure D.3).

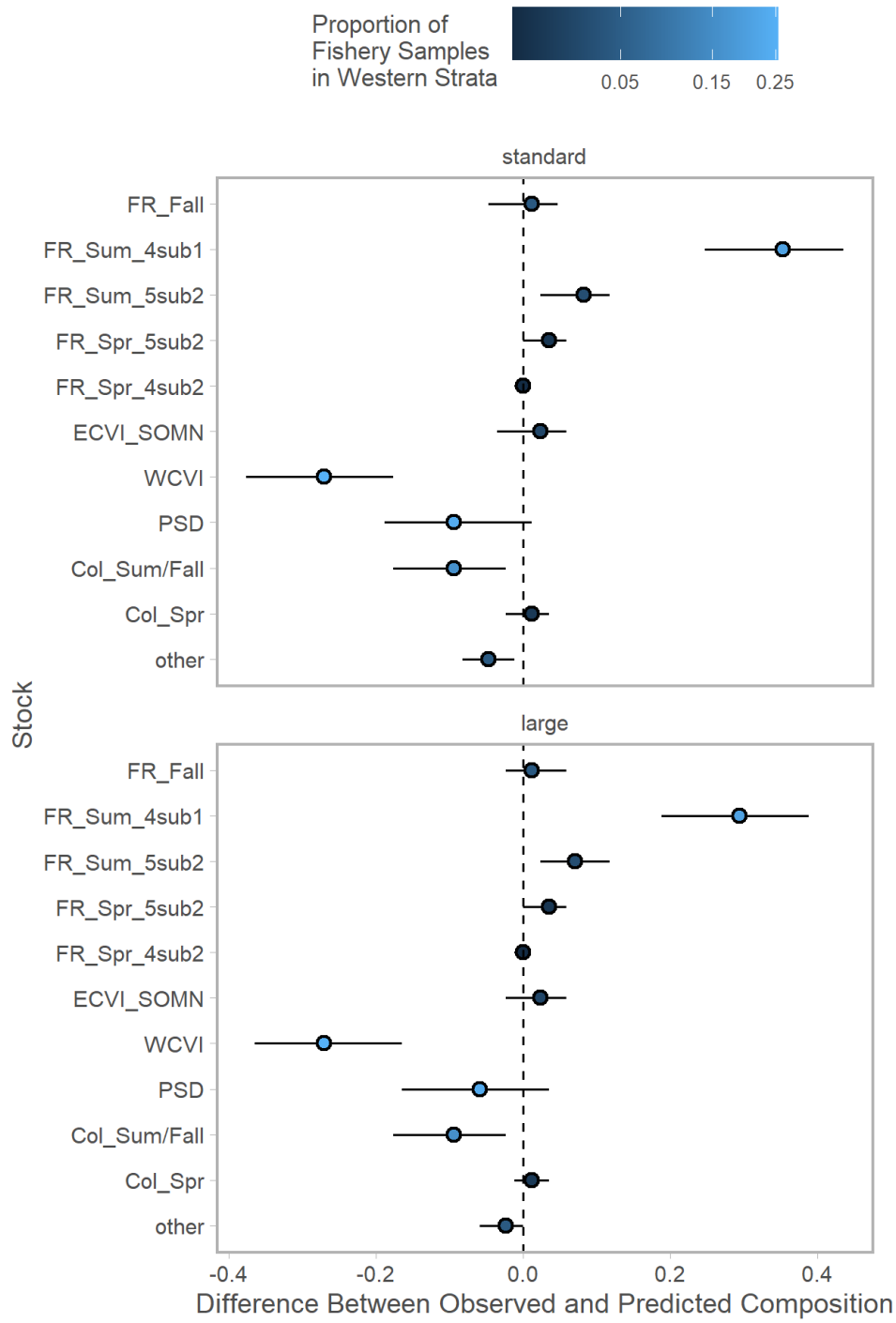

Figure D.3. Differences between the observed and model predicted contribution of each stock to SRKW prey remains using the standard model presented in the main text (top) and a model fit to data excluding individuals smaller than 75 cm fork length (bottom). Positive (negative) values indicate a given stock was observed more (less) frequently in SRKW prey remains than predicted by the fishery-dependent model. Points represent medians and whiskers represent 95th percentile intervals among 500 Monte Carlo simulations. Brighter (darker) points represent stocks that were more (less) common in recreational fishery samples from times and strata coincident with SRKW prey remains.

D.2. MANAGEMENT INTERVENTIONS

To evaluate the impact of management interventions on selectivity we removed prey samples from the simulation that were collected during times and locations when coincident fisheries were closed or impacted by maximum size limits. 11 prey samples were removed from the stock selectivity analysis and eight were removed from the size selectivity analysis. We then repeated the simulation analysis and compared the results to the original results presented in the main text.

Estimates of stock (Figure D.4) and size selectivity (Figure D.5) were qualitatively unchanged when a more conservative set of prey were included in the simulation. These results indicate that stock and size selectivity was not solely driven by the presence of management interventions. However, it is not possible to quantify the impact of management interventions throughout the study area on the model's estimates.

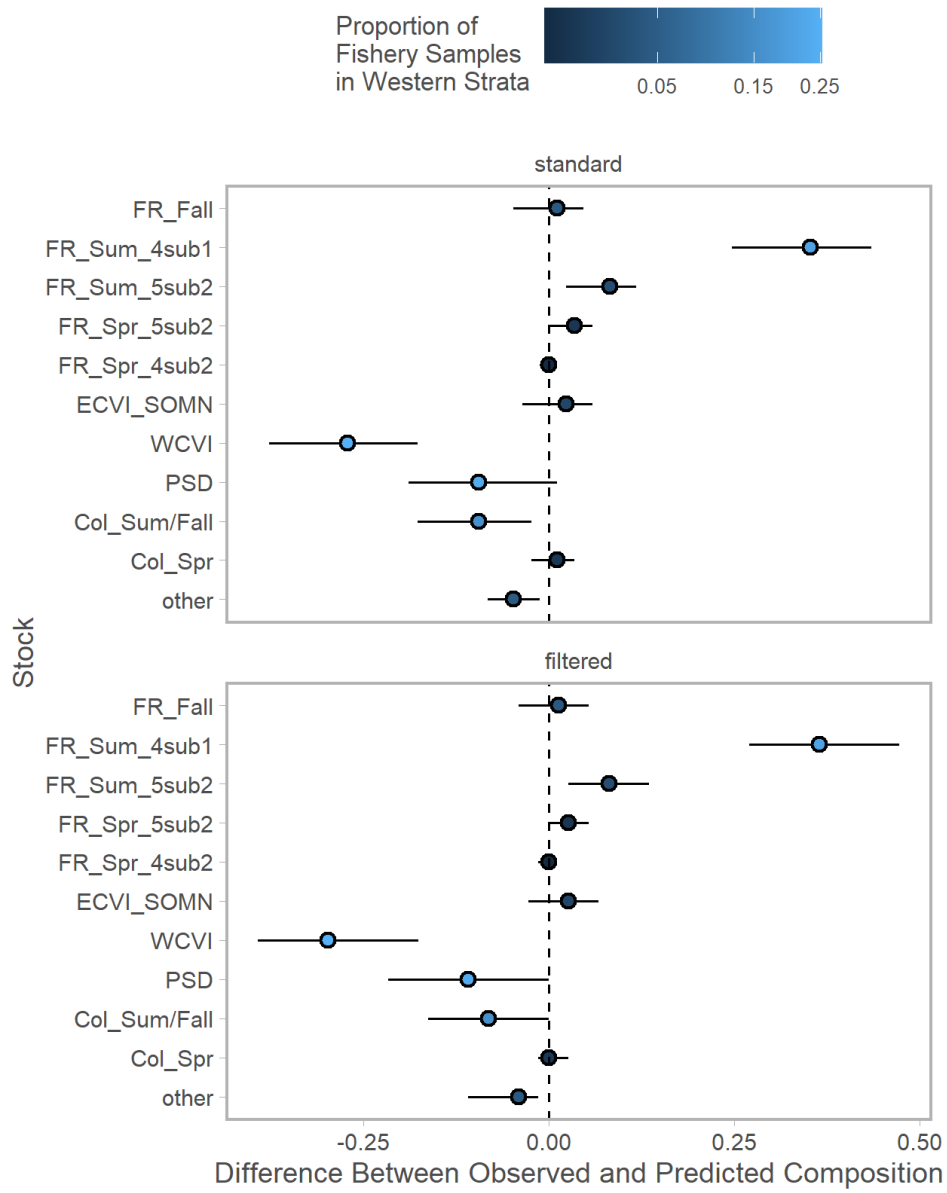

Figure D.4. Differences between the observed and model predicted contribution of each stock to SRKW prey remains using the full prey remains dataset presented in the main text (top) and prey remains that excluded samples collected in times and locations when management interventions were in place (bottom). Positive (negative) values indicate a given stock was observed more (less) frequently in SRKW prey remains than predicted by the fishery-dependent model. Points represent medians and whiskers represent 95th percentile intervals among 500 Monte Carlo simulations. Brighter (darker) points represent stocks that were more (less) common in recreational fishery samples from times and strata coincident with SRKW prey remains.

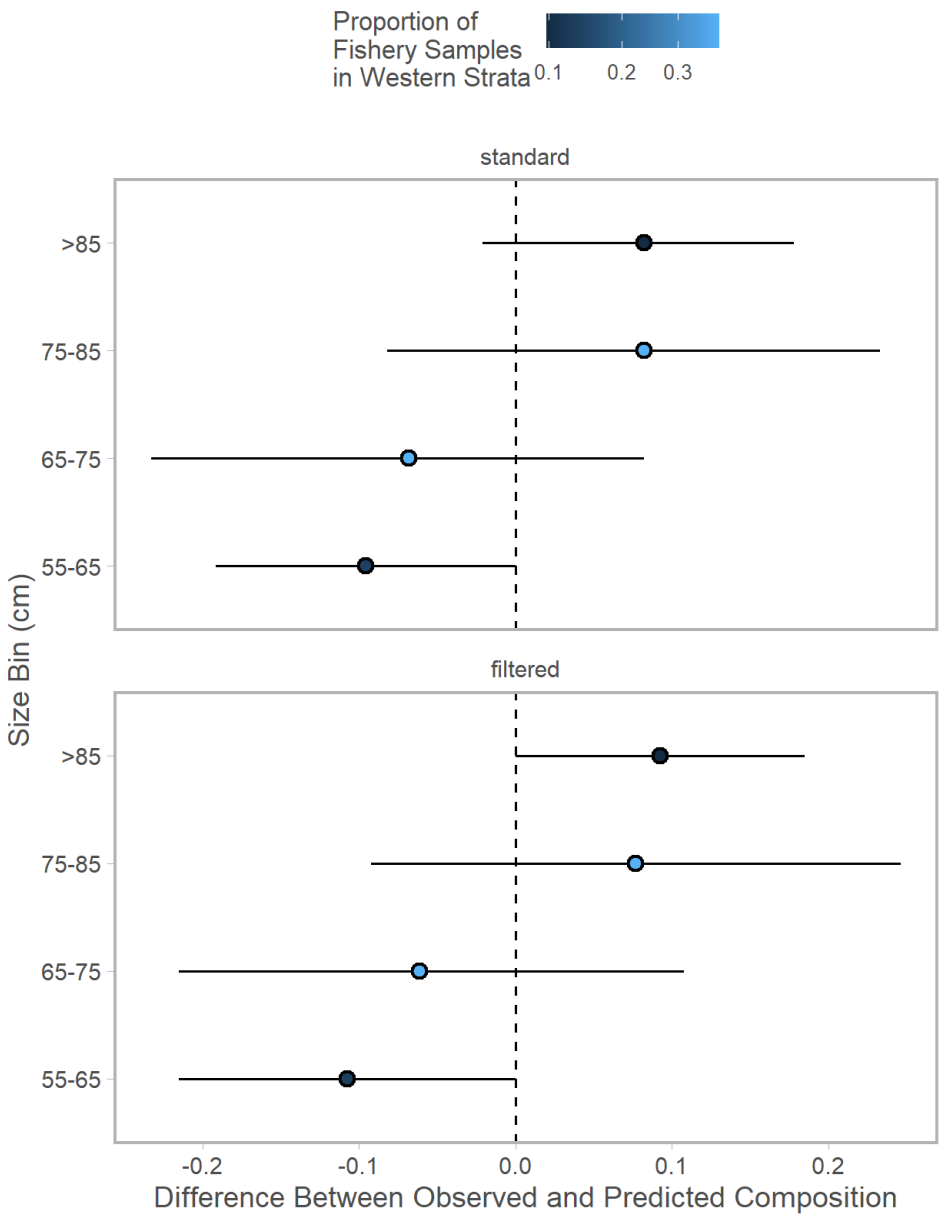

Figure D.5. Differences between the observed and model predicted contribution of each size class to SRKW prey remains using the full prey remains dataset presented in the main text (top) and prey remains that excluded samples collected in times and locations when management interventions were in place (bottom). Positive (negative) values indicate a given size class was observed more (less) frequently in SRKW prey remains than predicted by the fishery-dependent model. Points represent medians and whiskers represent 95th percentile intervals among 500 Monte Carlo simulations. Brighter (darker) points represent size classes that were more (less) common in recreational fishery samples from times and strata coincident with SRKW prey remains.