



**Abstract**—Pacific salmon (*Oncorhynchus* spp.) are important to the ecology, economy, and cultures of the Pacific Northwest. Many populations of Pacific salmon in the Pacific Northwest are declining because of poor marine survival. We evaluated the role of Steller (*Eumetopias jubatus*) and California (*Zalophus californianus*) sea lions as predators of Pacific salmon. Roughly, half of the 1330 metric tons (t) of Pacific salmon eaten by Steller sea lions per year and of the 1220 t of Pacific salmon eaten by California sea lions per year in northwest Washington during 2010–2013 were coho salmon (*O. kisutch*). The response of Steller and California sea lions to the large run of pink salmon (*O. gorbuscha*) in 2011 was less than expected. Sea lions of these species rarely ate large (roughly  $\geq 50$  cm in total length) Chinook salmon (*O. tshawytscha*), indicating that they have limited direct competition for prey with the southern resident distinct population segment of killer whales (*Orcinus orca*). Combined, California and Steller sea lions in northwest Washington consumed a mass of coho salmon similar to that landed by commercial fisheries in Washington State. More work on modeling the effect of the predation by California and Steller sea lions on salmon populations, particularly for coho salmon, is needed to better evaluate the conservation and productivity of Pacific salmon.

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## Consumption of Pacific salmon (*Oncorhynchus* spp.) by California sea lions (*Zalophus californianus*) and Steller sea lions (*Eumetopias jubatus*) in northwest Washington during 2010–2013

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Pacific salmon (*Oncorhynchus* spp.) are keystone species in the ecology (Willson and Halupka, 1995; Lincoln et al., 2020), economy (Amberson et al., 2016), and cultures (Butler and Campbell, 2004; Amberson et al., 2016; Korzow Richter et al., 2020; Atlas et al., 2021) of the Pacific Northwest. These species are taken by many predators (Willson and Halupka, 1995; Lincoln et al., 2020) throughout their life cycle and are important because they deliver marine-derived nutrients to freshwater (Zhang et al., 2003) and terrestrial ecosystems (Schindler et al., 2003; Walsh et al., 2020).

Many stocks of Pacific salmon along the West Coast of the United States are currently imperiled, and their important role in Pacific Northwest ecosystems is threatened (O'Higgins, 2015). Results from recent research indicate that the marine life phase of Pacific salmon plays a more important role in salmon population dynamics than had been previously recognized (Sobocinski et al., 2021; Welch et al., 2021). During

the marine life phase, survival of species of Pacific salmon is affected by climatic conditions (Mueter et al., 2005; Crozier et al., 2021), interspecific and intraspecific competition with other Pacific salmon (Ruggerone and Nielsen, 2004; Kendall et al., 2020), and predators (Chasco et al., 2017a; Seitz et al., 2019; Sherker et al., 2021). Across the North Pacific Ocean, Pacific salmon are becoming smaller and are more frequently spawning at younger ages (Ohlberger et al., 2018; Losee et al., 2019), reducing their reproductive potential (Ohlberger et al., 2020; Oke et al., 2020). Manishin et al. (2021) found that these changes observed in the demographic structure of Chinook salmon (*O. tshawytscha*) could be attributed to recent increases in the mortality rate of salmon in the life stage after their first winter in the ocean and suggested that high predation rates could be a major factor in mortality. More research is needed to improve our understanding of where and when predation of Pacific salmon occurs, particularly for recovery efforts

of evolutionary significant units of salmon listed as threatened or endangered under the U.S. Endangered Species Act (ESA) (Federal Register, 1999).

In northwest Washington from 2010 through 2013, Pacific salmon made up 11.7% of the diet of Steller sea lions (*Eumetopias jubatus*) and 13.5% of the diet of California sea lions (*Zalophus californianus*), and estimates of the consumption of Pacific salmon were 1330 and 1220 metric tons (t) per year for Steller and California sea lions, respectively (Scordino et al., 2022). Counts of Steller and California sea lions in northwest Washington increased 7.9% and 7.8% per year during 2010–2018 (Allyn and Scordino, 2020). The rise in abundance of these sea lion species likely has led to a doubling of the levels of consumption of Pacific salmon estimated by Scordino et al. (2022) for Steller and California sea lions over the past decade. The method of prey identification used by Scordino et al. (2022) could not be used to reliably identify salmon to the species level (Purcell et al., 2004; Korzow Richter et al., 2020), preventing evaluation of consumption of salmon by species.

The objective of this study was to conduct genetic analysis of the salmon bones used in the work reported in Scordino et al. (2022) to determine the seasonal and annual consumption of Pacific salmon by species and size class for California and Steller sea lions in northwest Washington. Determining the species and size class of Pacific salmon consumed by these species will allow improvements in modeling of effects of this predation on species of Pacific salmon and of the competition between fisheries and Steller and California sea lions (Chasco et al., 2017a, 2017b). This information will also help in evaluation of the hypothesis by Hilborn et al. (2012) that predation by sea lions and other predators on large Chinook salmon ( $\geq 50$  cm in total length [TL]) reduces the availability of this resource to killer whales (*Orcinus orca*) of the endangered southern resident distinct population segment (Federal Register, 2005) that depend on large Chinook salmon as their primary prey (Ford et al., 1998, 2016; Hanson et al., 2021). A second objective of the study described here was to document how California and Steller sea lions responded to the large increase in the number of Pacific salmon present in 2011 due to the large odd-year run of pink salmon (*O. gorbuscha*) (Losee et al., 2019).

## Materials and methods

### Sample collection

All scat samples analyzed in this study were collected at haul-out sites used by California and Steller sea lions in northwest Washington (Fig. 1), as reported by Scordino et al. (2022). Site selection for scat collections depended on distributions of California and Steller sea lions and on the ability of researchers to land safely at sites. Samples of Steller sea lion scat were collected primarily from haul-out sites in the Tatoosh Island Complex in the winter and spring and from Sea Lion Rock in the summer and fall;

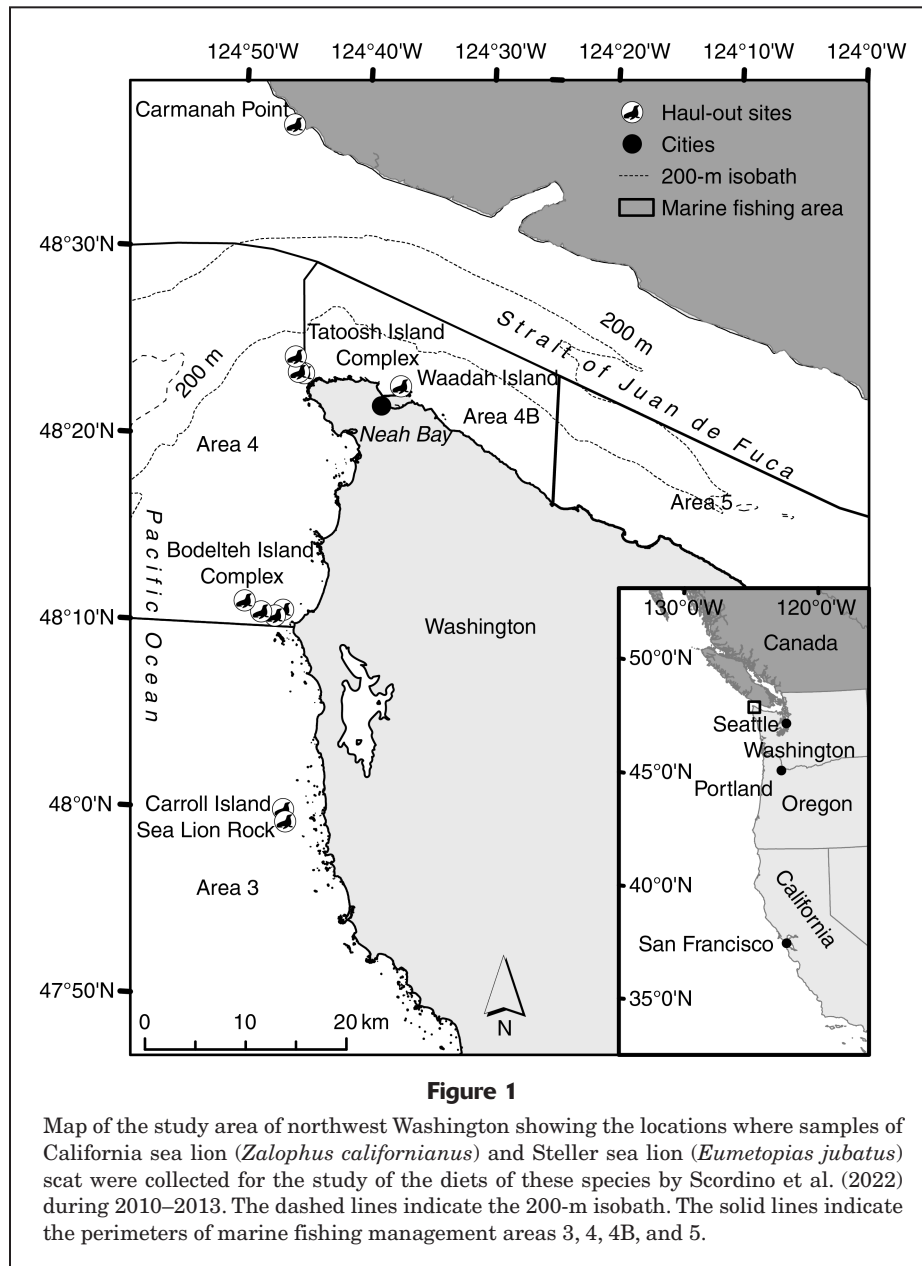
scats were obtained monthly between August 2010 and February 2013 as conditions allowed. Samples of California sea lion scat were collected primarily from East Bodelteh Island in the Bodelteh Island Complex and only in the spring, summer, and fall (Table 1).

### Processing of salmon bones

Scat samples were cleaned either by washing them in paint strainer bags in a residential-style washing machine or by washing them through nested sieves (Orr et al., 2003). After cleaning, hard parts from the scat were hand-picked from the paint strainer bag or sieves and placed in a glass vial with 70% isopropyl alcohol. Hard parts were then air-dried in a heated room. S. Riemer of the Oregon Department of Fish and Wildlife identified prey hard parts to the lowest taxonomic level possible on the basis of comparisons with a reference collection of fish and cephalopod hard parts from the region (Scordino et al., 2022). Salmon bones were identified to the family level because salmon bones cannot reliably be identified to species by using morphological features (Korzow Richter et al., 2020). Identified salmon bones were separated from the rest of the prey hard parts into gelatin capsules for subsequent analysis.

Salmon bones were sorted by the size of salmon consumed on the basis of a comparison to a reference collection of salmon from estuaries and coastal areas of the Pacific Northwest. Bones from salmon consumed during their first year in the ocean, fish that were roughly less than 25 cm TL (Duffy and Beauchamp, 2011), were assigned to the small size class of salmon. The large size class of salmon corresponded with the size range of returning adult salmon, fish that were roughly 50 cm TL and greater. Recovered salmon bones that could not be definitely sorted to the large or small size class, because the bone had eroded during digestion or because the recovered type of bone (e.g., gill rakers) is known to have a wide range of sizes within a fish, were recorded as salmon of unclassified size. This unclassified size class also includes medium-sized salmon ranging roughly from 25 to 50 cm TL. Our reporting of recovered bones from salmon in the small and large size classes are minimum estimates because an unknown proportion of the unclassified size class was composed of small and large salmon.

We selected 2–3 representative salmon bones from each size class in each scat sample for genetic analysis. In the genetic analysis, a single bone from each size class was used for species determination. If the sample failed to amplify sufficiently for species identification, another representative bone was analyzed. Our research method required the assumption that the sea lions ate only 1 species of salmon per each size class of salmon observed in a scat sample because we did not have enough funding to analyze all of the salmon bones found in scat samples from the Scordino et al. (2022) study. This assumption likely is not valid given that a previous study found more than one species of salmon present in the gastrointestinal tract of 3 of 28 sea lions sampled (Roffe and Mate, 1984).



### Genetic analysis

Salmon bones were pulverized in a BeadBug<sup>1</sup> homogenizer (SKU D1030, Benchmark Scientific, Sayreville, NJ) by using 2-mL prefilled sterile tubes containing 3-mm zirconium beads (SKU D1032-30, Benchmark Scientific). Pulverized bone samples were then digested for 24 h at 56°C in 500 µL of extraction buffer (0.5 M EDTA pH 8, 1 M urea, and 20 mg/µL proteinase K) with constant rotation. After 24 h, digested samples were centrifuged at 1000 g for 5 min to pellet bone material. After centrifugation, the

<sup>1</sup> Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

supernatant lysate was carefully pipetted into sterile 15-mL falcon tubes, and DNA was purified from the supernatant lysate by using a QIAquick PCR purification kit (catalog no. 28104, Qiagen, Hilden, Germany). To increase DNA yield, the elution buffer was heated to 60°C prior to it being added to the column during the elution step.

We used species-specific primers and Applied Biosystems TaqMan MGB probes (minor groove binder probes, Thermo Fisher Scientific, Waltham, MA) developed by Rasmussen Hellberg et al. (2010) for identifying salmon bones as chum salmon (*O. keta*), Chinook salmon, pink salmon, steelhead (*O. mykiss*), sockeye salmon (*O. nerka*), or coho salmon (*O. kisutch*) on the basis of 915 cytochrome *c* oxidase subunit I DNA barcode sequences (Table 2). No TaqMan MGB probes were used for cutthroat trout

**Table 1**

Summary of the sampling of Steller sea lion (*Eumetopias jubatus*) and California sea lion (*Zalophus californianus*) scat conducted by Scordino et al. (2022) from 2010 through 2013 in northwest Washington by year, season, and month.

Species	Year	Spring			Summer			Fall			Winter			Total
		Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	
Steller sea lion	2010	0	0	0	0	0	32	3	0	27	0	0	0	62
	2011	48	18	24	35	36	42	4	31	36	0	38	0	312
	2012	38	35	34	28	36	38	35	22	38	8	0	39	351
	2013	0	0	0	0	0	0	0	0	0	0	34	17	51
California sea lion	2010	0	0	0	0	0	0	42	0	0	0	0	0	42
	2011	0	0	47	2	0	0	0	0	51	0	0	0	100
	2012	0	0	0	48	0	0	51	22	0	0	0	0	121

**Table 2**

Species-specific primers used to identify bones of Pacific salmon (*Oncorhynchus* spp.), found in scat of Steller sea lions (*Eumetopias jubatus*) and California sea lions (*Zalophus californianus*), to species by using real-time polymerase chain reactions. Scat samples were collected in northwest Washington from 2010 through 2013. Forward (F) and reverse (R) primers developed by Rasmussen Hellberg et al. (2010) and TaqMan minor groove binder probes were used. bp=base pair.

Species	Primer or probe	Sequence (5'-3')	Amplicon size
Chum salmon	F	TTGTCTGAGCTGTACTAATCACTG	104 bp
	R	AAGTGGTGTTTAAATTTTCGATC	
	P	VIC-CAACATAGTAATACCTGCTG-MGB	
Chinook salmon	F	GATAGTAGGCACCGCCCTTAGT	183 bp
	R	CCGATCATTAGGGGAATTAATCAGT	
	P	NED-TCATAATCGGCATAACTAT-MGB	
Pink salmon	F	TACGACCATTATCAACATAAAACCA	143 bp
	R	GGTCCGTGAGCAACATAGTG	
	P	6FAM-CGGCAATCTCTCAGT-MGB	
Steelhead	F	ACCATTATTAACATAAAACCTCCAG	121 bp
	R	GTAATGCCTGCTGCCAGG	
	P	VIC-CGTTTGAGCCGTGCTA-MGB	
Sockeye salmon	F	GGAAACCTTGCCACGCG	152 bp
	R	AAAAGTGGGGTCTGGTACTGAG	
	P	6FAM-CTCTGTTGACTTAACCATC-MGB	
Coho salmon	F	CGCTCTTCTAGGGGATGATC	95 bp
	R	CTCCGATCATAATCGGCATG	
	P	VIC-ATTTACAACGTAATCGTC-MGB	

(*O. clarkii*) or bull trout (*Salvelinus confluentus*) because they are not common in the study area relative to other salmonids (Brenkman and Corbett, 2005; Percy et al., 2018) and because a TaqMan MGB probe has not been developed for these species (Rasmussen Hellberg et al., 2010).

An optimized multiplexed TaqMan presence-absence assay was performed in triplicate on all purified DNA samples by using an Applied Biosystems StepOnePlus

Real-Time PCR System (catalog no. 4376787, Thermo Fisher Scientific). Primer concentrations were 900 nM, and probe concentrations were 250 nM. Each run was accompanied by internal positive and negative controls. Analysis was performed by using Applied Biosystems StepOne Real-Time PCR Software, vers. 2.0 (Thermo Fisher Scientific) built into the StepOnePlus Real-Time PCR System. This software was run by using a presence-absence setting that

works by measuring the intensity of the fluorogenic signal from the species-specific probes. The threshold for a positive identification was set by the StepOne software to the exponential phase of the amplification curve. Samples of salmon bones that had a single species read past a set threshold of fluorogenic signal intensity were recorded as a positive read for the species identified. Samples with no amplification or multiple signals were recorded as unidentified salmon. All parameters were set to best accommodate all primer temperature sensitivities with the optimized annealing temperature of 53°C (Rasmussen Hellberg et al., 2010).

### Assessment of genotyping accuracy

We conducted a blind study of 15 samples of known Pacific salmon species provided by the NOAA Northwest Fisheries Science Center to evaluate our genotyping error rate. We provided the samples to our laboratory team (C. Marshall, R. James, and D. Shay) at the Institute of Science and Technology of North Central High School in Spokane, Washington, with unique identifiers that did not identify the species of salmon of the sample. The laboratory team ran the samples along with the salmon bones collected from samples of California and Steller sea lion scat.

### Data analysis

Species of Pacific salmon identified as prey in scat samples and their size classes were tabulated for each sample. We combined the results from our genetic analysis with the sea lion diet data available from Scordino et al.<sup>2</sup> to calculate the split-sample frequency of occurrence (SSFO) of Pacific salmon by size class, species, and combination of species and size class. We calculated SSFO twice. In the first calculation, we included a species category of *unidentified salmon*. For the second calculation of SSFO, we assumed that the salmon bones identified in our work were a representative sample of unidentified salmon bones and incorporated the unidentified bones into data for identified prey species proportionally according to identifications within each salmon bone size class.

The following formula was used to calculate SSFO:

$$SSFO_i = \frac{\sum_{k=1}^i (O_{ik} / O_k)}{s} \times 100,$$

where  $O_{ik}$  = 0 if taxon  $i$  is absent in scat sample  $k$  and 1 if taxon  $i$  is present in scat sample  $k$ ,

$O_k$  = total number of all taxa present in scat sample  $k$ ; and

$s$  = total number of scat samples that contained prey (Olesiuk et al., 1990).

In many studies, SSFO has been used to reconstruct pinned diets (Olesiuk et al., 1990; Tollit et al., 2015), but it does have the potential to overreport the importance of

small prey and underreport the importance of large prey (Laake et al., 2002; Tollit et al., 2007). The resultant SSFO values were multiplied by the prey consumption estimates for California and Steller sea lions by Scordino et al. (2022) to provide an estimate of annual biomass of Pacific salmon consumed by species, by size class, and by species and size class during 2010–2013 in northwest Washington.

We used Pearson's chi-square ( $\chi^2$ ) and Fisher's exact tests to evaluate differences in the species and size composition of Pacific salmon consumed. First, we compared consumption of each Pacific salmon species by season and year within the diet of each sea lion species and between the diets of the 2 species of sea lions. Second, we evaluated differences in the size-class composition of Pacific salmon consumed by season and year within the diet of each sea lion species and between the diets of the 2 species. For yearly comparisons between species, only samples collected in spring, summer, and fall were used because no samples of California sea lion scat were collected during winter. Annual comparisons of Pacific salmon consumed for each species included only data for 2011 and 2012 because samples were collected in all seasons during those years. For analyses of the species composition of Pacific salmon consumed, only samples identified to species were used; we excluded unidentified salmon from these analyses.

### Comparison of salmon consumption by sea lions to fishery landings

For the period from 2010 through 2013, we downloaded commercial salmon fishery data from the Pacific Fisheries Information Network APEX reporting system (available from [website](#)). The data comprise commercial landings records from both the treaty tribal fisheries and non-treaty fisheries. We calculated the average annual commercial catch of Pacific salmon from 2010 through 2013 for coastal Washington (ports along the Pacific coast, estuaries, and Neah Bay) and for all of Washington State to compare commercial catch to estimates of consumption of Pacific salmon by California and Steller sea lions.

### Results

Genetic analysis was conducted on 361 samples of bones identified as those of Pacific salmon by Scordino et al. (2022). Bone samples were from 330 samples of California (93 bone samples, 89 scat samples) and Steller (268 bone samples, 241 scat samples) sea lion scat. For 4 samples of California sea lion scat and 27 samples of Steller sea lion scat, 2 size classes of salmon were identified; for all other scat samples, a single size class of salmon was identified. All data evaluated in the research described in this paper are publicly available (Scordino et al.<sup>3</sup>).

<sup>2</sup> Scordino, J., A. Akmajian, and S. Riemer. 2021. Steller and California sea lion count and diet data in northwest Washington, 2010–2013. Mendeley Data, V1. [Available from [website](#).]

<sup>3</sup> Scordino, J., A. Akmajian, C. Marshall, S. Riemer, R. James, and D. Shay. 2022. Diets of Steller and California sea lions determined from scat collections in northwest Washington during 2010–2013 with genetic identification of salmon species. Mendeley Data, V2. [Available from [website](#).]



Of the scat from California sea lions, 37 samples had remains of Pacific salmon in the large size class, 10 samples had bones of salmon in the small size class, and 46 samples had bones from salmon of an unclassified size. Of the scat from Steller sea lions, 53 samples had remains of Pacific salmon in the large size class, 59 samples had bones of salmon in the small size class, and 156 samples had bones from salmon of an unclassified size. We found a significant difference in the proportion of Pacific salmon of each size class consumed between California and Steller sea lions by pooling samples from spring, summer, and fall (Pearson's  $\chi^2=6.64$ ,  $df=2$ ,  $P=0.036$ ). California sea lions more frequently ate large salmon and less frequently ate small salmon in comparison with Steller sea lions.

Through our genetic analysis, the species was determined for 305 of the 361 salmon bones analyzed (84.5%) (Table 3). For both California and Steller sea lions, coho salmon was the most frequently identified salmon species in all 3 size classes (Table 3). Pooling bones of Pacific salmon in all size classes from scat samples collected in the spring, summer, and fall, we found significant differences in the composition of Pacific salmon species consumed by California and Steller sea lions (Pearson's  $\chi^2=13.22$ ,  $df=5$ ,  $P=0.021$ ).

Both California and Steller sea lions had significant differences in the composition of Pacific salmon species they consumed by season, with all size classes of Pacific salmon pooled (Suppl. Table 1; Steller sea lion:  $\chi^2=98.2$ ,  $df=2$ ,  $P<0.0001$ ; California sea lion:  $\chi^2=22.7$ ,  $df=10$ ,  $P=0.012$ ). Coho salmon was the most frequently identified salmon species in samples of California sea lion scat collected in fall and winter; chum and pink salmon were the most commonly identified species from samples collected in spring. Coho salmon was the most frequently identified salmon species in samples of Steller sea lion scat collected in the fall, spring, and winter; the majority of salmon bones identified from samples collected in summer were pink salmon. We found no significant differences by size class

in the species composition of Pacific salmon consumed by California and Steller sea lions (Suppl. Table 2).

We tested the responses of California and Steller sea lions to the large increase of pink salmon available in 2011 (Losee et al., 2019) by comparing the species composition of Pacific salmon consumed between 2011 and 2012. We found no significant difference in the annual species composition of Pacific salmon consumed by Steller sea lions in 2011 and 2012. We further compared Pacific salmon consumption between years by using only samples collected in summer because commercial fishery landings of adult pink salmon are typically highest in the study area in the summer. We found inconclusive but suggestive evidence of differences in the composition of Pacific salmon species consumed between summer 2011 and summer 2012 (Fisher's exact test:  $P=0.058$ ), with pink salmon accounting for a larger percentage of the salmon consumed in 2011 than in 2012. We had to limit our analysis of the response of California sea lions to samples collected in the fall in 2010, 2011, and 2012 because samples were not collected in spring and summer in all years (Table 1). We found significant differences in the composition of Pacific salmon species identified by year (Fisher's exact test:  $P<0.001$ ), with coho salmon being the dominant species among species identified in 2010 and 2012 and chum salmon being the dominant identified species in 2011.

#### Salmon consumption estimates

Data on salmon species identified from the genetic analysis in this study was combined with data on the diets of California and Steller sea lions from Scordino et al.<sup>2</sup> to compute the SSFO by Pacific salmon species identified and for unidentified salmon by size class. We assumed that our calculated SSFO was equivalent to percentage of diet (Olesiuk et al., 1990). Coho salmon composed the largest portion of the diets of California and Steller sea lions among the Pacific salmon species identified in scat

**Table 3**

Species composition of salmonids (*Oncorhynchus* spp.) identified in scat samples of California sea lions (*Zalophus californianus*) and Steller sea lions (*Eumetopias jubatus*) collected in northwest Washington from 2010 through 2013 by size class and associated sample size of identified salmon and unidentified (Unid.) bones. The size classes of prey species are large ( $\geq 50$  cm in total length [TL]), small ( $< 25$  cm TL), and unclassified (could not be definitely sorted to the large or small size class).

Predator species	Size class	Prey species identified						Sample size	
		Coho	Chum	Chinook	Steelhead	Pink	Sockeye	Unid.	Identified
California sea lion	All classes	46.4%	27.4%	7.1%	3.6%	11.9%	3.6%	9	84
	Large	54.3%	22.9%	5.7%	2.9%	8.6%	5.7%	2	35
	Unclassified	43.6%	30.8%	7.7%	2.6%	15.4%	0.0%	7	39
	Small	30.0%	30.0%	10.0%	10.0%	10.0%	10.0%	0	10
Steller sea lion	All classes	57.0%	13.6%	9.5%	10.9%	8.6%	0.5%	47	221
	Large	47.7%	20.5%	6.8%	11.4%	13.6%	0.0%	9	44
	Unclassified	54.3%	14.2%	8.7%	14.2%	7.9%	0.8%	29	127
	Small	72.0%	6.0%	14.0%	2.0%	6.0%	0.0%	9	50

samples (Fig. 2). Multiplying SSFO by the estimates of consumption computed by Scordino et al. (2022), we found that Steller sea lions ate an average of 714.1 t of coho salmon per year and that California sea lions ate 550.4 t of coho salmon from spring through fall during 2010–2013 (Table 4). Chinook salmon composed 0.8% of the diet of both California and Steller sea lions (Suppl. Table 3), with average estimates of consumption of 93.6 t per year for Steller sea lions and of 74.1 t for California sea lions from spring through fall during 2010–2013 (Table 4). Proportionally assigning unidentified salmon bones to a salmon species on the basis of the frequency it was identified, we computed that Steller sea lions ate an average of 861.7 t of coho salmon and 116.4 t of Chinook salmon per year and that California sea lions ate 601.0 t of coho salmon and 80.9 t of Chinook salmon from spring through fall in each year (Suppl. Table 4).

#### Blind study of identification accuracy

Fifteen samples were provided to our laboratory team for a blind analysis of identification accuracy. The team was able to identify the species for 13 of the 15 samples, and the identification was accurate for all 13 samples.

#### Comparison of salmon consumption by sea lions to fishery landings

We compared consumption of each Pacific salmon species by California and Steller sea lions to commercial fisheries landings of Pacific salmon on the coast of Washington and in all of Washington State (Table 5). Steller sea lions consumed more coho salmon, chum salmon, pink salmon, and steelhead than were landed in commercial fisheries at coastal ports in Washington. In addition to the species

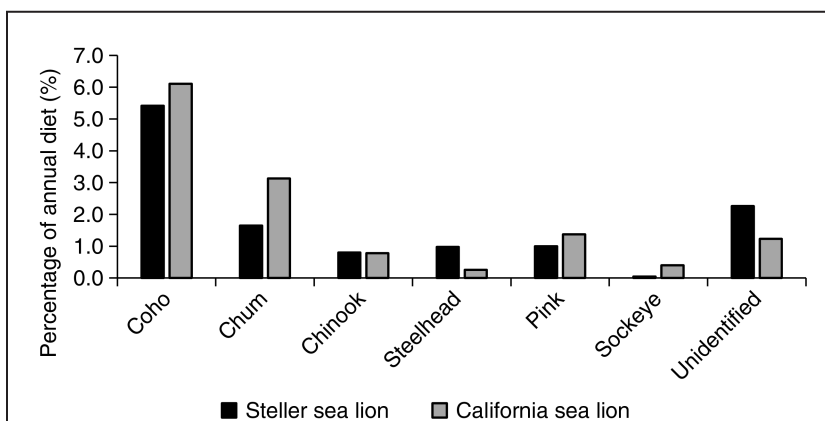
listed for Steller sea lions, California sea lions also consumed more sockeye salmon per year than were landed in commercial fisheries in coastal Washington. In contrast, the combined estimates of consumption for both species of sea lions for Chinook salmon of all size classes was roughly 8.5 times less than the commercial landings of Chinook salmon in coastal Washington. To compare consumption to statewide commercial fishery landings, we combined the consumption estimates for California and Steller sea lions for all size classes of Pacific salmon. We found that California and Steller sea lions eat more steelhead than are landed in commercial fisheries throughout the state of Washington. The total estimated consumption of all size classes of coho salmon by California and Steller sea lions of 1462.8 t is similar to the statewide landings by the commercial fishery of 1646.8 t.

Fisheries generally target Pacific salmon that we would classify as large salmon in our study of consumption of salmon by California and Steller sea lions. Commercial fisheries on the Pacific coast of Washington landed more Pacific salmon of each species, with the exception of sockeye salmon, than our minimum estimate of consumption of large Pacific salmon by sea lions (Table 5).

#### Discussion

This study is the first to rigorously evaluate consumption of Pacific salmon by California and Steller sea lions in Washington State. We found significant differences between California and Steller sea lions in the size class of Pacific salmon consumed, with Steller sea lions more frequently consuming salmon in the small size class despite being the larger of the 2 sea lion species (Wynne, 1993). Coho salmon was the most frequently consumed salmon for both California and Steller sea lions. This result was not surprising for small Pacific salmon because coho salmon are the most abundant juvenile salmon off the coast of Washington, followed by Chinook salmon (Percy and Fisher, 1990). In addition to being more abundant, juvenile coho salmon are typically distributed at shallower depths in the water column than the depths at which Chinook salmon are found (Beamish et al., 2018), likely increasing their vulnerability to predation by sea lions. When consuming large Pacific salmon, California and Steller sea lions most frequently consumed coho salmon despite the greater abundance of returning adult pink, sockeye, and chum salmon migrating through the study area (Losee et al., 2019; Walters et al., 2020).

The total mass of coho salmon consumed by California and Steller sea lions in northwest Washington was similar to the mass of coho salmon landed by



**Figure 2**

Split-sample frequency of occurrence of salmon species identified in samples of California sea lion (*Zalophus californianus*) and Steller sea lion (*Eumetopias jubatus*) scat collected in northwest Washington from 2010 through 2013. The *Unidentified* category is for salmon bones found in scat samples that we were unable to identify to species through genetic analysis.

**Table 4**

Estimated average seasonal consumption of salmon in metric tons (t) by Steller (*Eumetopias jubatus*) and California (*Zalophus californianus*) sea lions, by size class of prey and season during 2010–2013 in northwest Washington. Species of salmon were identified by analyzing bones found in sea lion scat. The size classes are small (<25 cm in total length [TL]), large (≥50 cm TL), and unclassified. The total consumption estimates for California sea lions are partial-year estimates from spring through fall (no scat of California sea lions was collected in winter). Consumption of the family Salmonidae is informed by the split-sample frequency of occurrence (SSFO) of prey taxa. The consumption of individual salmon species within size classes is informed by the SSFO of prey identified to the lowest possible taxon, with species of different size classes treated as unique species. As a result, the estimated total consumption of individual species does not equal the total estimated consumption of the family Salmonidae.

Taxon	Consumption by Steller sea lions (t)					Consumption by California sea lions (t)			
	Spring	Summer	Fall	Winter	Annual	Spring	Summer	Fall	Spring–fall
Salmon (Salmonidae)	377.1	116.2	577.0	387.6	1457.9	185.8	183.9	835.1	1204.8
Small size class	93.1	18.0	51.0	121.0	283.1	20.1	3.5	51.9	75.6
Coho salmon	60.5	4.7	22.4	88.2	175.9	0.0	3.5	15.8	19.4
Chum salmon	4.1	0.0	8.2	0.0	12.3	0.0	0.0	26.6	26.6
Chinook salmon	18.1	7.4	0.0	0.0	25.5	4.4	0.0	0.0	4.4
Steelhead	0.0	0.0	0.0	6.2	6.2	7.0	0.0	0.0	7.0
Pink salmon	0.0	3.0	0.0	10.9	13.9	0.0	0.0	9.5	9.5
Sockeye salmon	0.0	0.0	0.0	0.0	0.0	8.8	0.0	0.0	8.8
Unidentified	10.4	3.0	20.4	15.6	49.3	0.0	0.0	0.0	0.0
Unclassified	263.8	53.2	324.6	291.3	932.9	141.6	129.6	301.5	572.7
Coho salmon	120.1	6.6	114.2	159.3	400.2	43.8	58.1	107.7	209.6
Chum salmon	11.3	11.8	90.7	20.0	133.8	39.4	0.0	130.5	169.9
Chinook salmon	34.7	0.0	14.6	6.2	55.6	0.0	0.0	38.0	38.0
Steelhead	21.5	0.0	42.5	41.3	105.3	0.0	5.6	0.0	5.6
Pink salmon	8.1	19.9	10.4	15.6	54.1	40.9	21.2	12.7	74.7
Sockeye salmon	0.0	0.0	0.0	6.2	6.2	0.0	0.0	0.0	0.0
Unidentified	68.1	14.8	52.2	42.7	177.7	17.5	44.7	12.7	74.9
Large size class	37.0	46.4	222.8	7.8	314.0	26.3	49.4	463.6	539.3
Coho salmon	20.3	6.9	110.8	0.0	138.0	0.0	21.2	300.2	321.4
Chum salmon	0.0	4.4	72.3	0.0	76.7	8.8	14.1	70.3	93.2
Chinook salmon	7.3	0.0	5.2	0.0	12.5	0.0	0.0	31.7	31.7
Steelhead	9.5	2.2	0.0	7.8	19.5	8.8	0.0	0.0	8.8
Pink salmon	0.0	18.0	5.2	0.0	23.2	8.8	14.1	7.6	30.5
Sockeye salmon	0.0	0.0	0.0	0.0	0.0	0.0	0.0	28.5	28.5
Unidentified	0.0	14.8	29.2	0.0	44.0	0.0	0.0	25.3	25.3

commercial fisheries throughout the state of Washington. Roughly half of the population of Steller sea lions in Washington State haul out in our study area (Scordino et al.<sup>4</sup>). Furthermore, the positive trend in counts at haul-out sites in northwest Washington (Allyn and Scordino, 2020) indicates that the abundance of California and Steller sea lions has more than doubled over the past decade, and their consumption of Pacific salmon has likely also doubled. Therefore, the total mass of coho salmon consumed by California and Steller sea lions in all of Washington is likely much greater than is landed in commercial

fisheries. Future efforts to model marine survival of coho salmon would benefit from inclusion of the abundance of California and Steller sea lions.

Prior to conducting our study, we hypothesized that consumption of Pacific salmon by California and Steller sea lions would be greatest during the summer of odd-numbered years, when large runs of pink salmon are available. Contrary to that expectation, the season with the lowest overall salmon consumption by Steller sea lions was summer, when many adult Pacific salmon, including pink salmon, migrate through the study area. Furthermore, Pacific salmon accounted for a smaller component of the diets of both California and Steller sea lions in 2011 than in 2012. Pink salmon were the most commonly consumed salmon by Steller sea lions during the summer, but not by as much as expected given that, during 2011, roughly 70% of the Pacific salmon returning to Puget Sound were pink salmon (Losee et al., 2019). This result is even more surprising given that results from previous diet

<sup>4</sup> Scordino, J. J., S. J. Jeffries, and B. A. Diehl. 2014. Steller sea lion aerial survey counts in Washington, Oregon, and northern California during the breeding season of 2011. *In* Research and education/outreach to benefit ESA listed and recently delisted marine mammals of northwest Washington (J. J. Scordino and A. M. Akmajian, eds.), p. 190–198. Final report for species recovery grant award NA10NMF4720372. [Available from Makah Fish. Manag., Makah Tribe, P.O. Box 115, Neah Bay, WA 98357.]



**Table 5**

Comparison of average commercial landings of salmon to salmon consumption by California sea lions (*Zalophus californianus*), Steller sea lions (*Eumetopias jubatus*), and both species combined, by species, from 2010 through 2013 in northwest Washington. Sea lion consumption estimates are reported separately for all and large ( $\geq 50$  cm in total length) size classes because only large salmon are targeted by commercial fisheries. Estimates of consumption by California sea lions are partial-year estimates that do not include consumption in winter.

Species	Sea lions in northwest Washington							
	Commercial landings		Steller		California		Both species	
	Coastal Washington	All of Washington	All classes	Large class	All classes	Large class	All classes	Large class
Chinook	406.7	2421.0	116.4	14.3	80.9	33.2	197.3	47.4
Chum	143.5	4819.4	271.1	87.5	316.4	97.5	587.5	185.0
Coho	548.3	1646.8	861.7	157.4	601.0	336.5	1462.8	493.9
Pink	67.4	4911.5	116.3	26.5	125.2	31.9	241.6	58.4
Sockeye	7.8	1646.6	7.2	0.0	40.7	29.8	47.9	29.8
Steelhead	84.7	169.7	157.1	22.2	23.4	9.2	180.5	31.4

studies indicate that pinnipeds typically eat fish less than 30 cm in length (Etnier and Fowler, 2010) and that pink salmon are the smallest Pacific salmon.

California and Steller sea lions ate over 2550 t of Pacific salmon per year during 2010–2013 in northwest Washington; therefore, it is logical to examine whether these 2 species of sea lions are affecting the species of Pacific salmon listed under the ESA. The Fishery Regulation Assessment Model is used to model stock-based effects of fisheries on coho and Chinook salmon on the basis of data from recovery of coded-wire tags (Moran et al., 2018). We ran the Fishery Regulation Assessment Model by using data for marine fishing management areas 3, 4, and 4B, areas designated by the Washington Department of Fish and Wildlife that include Carroll Island, Sea Lion Rock, the Tatoosh Island Complex, the Bodelteh Island Complex, and Waadah Island (Fig. 1). We used these data from these areas in 2010–2013 to determine what proportion of the large Chinook and coho salmon consumed by sea lions were likely to be from populations listed as threatened or endangered under the ESA. We assumed for the purpose of this model that California and Steller sea lions eat a composition of stocks of coho and Chinook salmon similar to the stock composition of Pacific salmon caught in fisheries. We found that roughly 3% of the large coho salmon and 5% of the large Chinook salmon in marine fishing management areas 3, 4, and 4B during 2010–2013 were from ESA-listed populations.

The effect of predation by California and Steller sea lions on ESA-listed populations of Chinook salmon is likely less than the effect of commercial fisheries given the disparity in the metric tons of Chinook salmon landed by the fisheries and the metric tons consumed by California and Steller sea lions (Table 5). In contrast, the effect of predation by California and Steller sea lions on ESA-listed populations of coho salmon likely exceeds the effect of commercial

fisheries for the reasons previously discussed. California and Steller sea lions may also be affecting the recovery of the threatened population of Lake Ozette sockeye salmon given its small size of 7000 returning adults during 2016–2019 (Haggerty<sup>5</sup>) and the proximity of the outfall of the Ozette River to the haul-out sites we surveyed. Ecosystem modeling that incorporates the direct effect of predation by sea lions on salmon as well as the effects on salmon predators and prey should be conducted to investigate the effect of California and Steller sea lions on populations of salmon in the Pacific Northwest.

A goal of this study was to evaluate if California and Steller sea lions in northwest Washington compete with endangered southern resident killer whales for their preferred prey of large Chinook salmon (Ford and Ellis, 2006; Hanson et al., 2021). We found that large Chinook salmon accounted for at least 0.3% and 0.1% of the diets of California and Steller sea lions, respectively. The small amount of large Chinook salmon consumed by California and Steller sea lions relative to the catch in sport and commercial fisheries in northwest Washington (Table 5) indicates that, in our study area, both species of sea lions are not major direct competitors with killer whales for prey. California and Steller sea lions likely have indirect effects on the availability of prey of killer whales because their predation on small- and medium-sized Chinook salmon reduces the number of Chinook salmon reaching the large size preferred by killer whales. The magnitude of this indirect effect is hard to evaluate because estimates of the number of Chinook salmon eaten are very sensitive to the estimated size of Chinook salmon consumed (Chasco et al., 2017a, 2017b; Nelson et al., 2021). Our size sorting allowed us to make broad interpretations of the size classes of Pacific salmon predated by

<sup>5</sup> Haggerty, M. 2022. Personal commun. Mike Haggerty Consulting, 242 Whiskey Creek Beach Rd., Port Angeles, WA 98363.

California and Steller sea lions, but the approach does not provide size estimates specific enough to allow computation of the number of Pacific salmon consumed. In future studies of the diets of sea lion species, all salmon bones should be measured to allow quantitative estimates of the size of salmon consumed.

Scordino et al. (2022) noted a number of caveats to their interpretation of their diet analysis that also apply to the results of this study. Most important of those caveats is that estimates from this study could overreport the consumption of small Pacific salmon and underreport the consumption of large Pacific salmon because of the use of SSFO to evaluate the diets of California and Steller sea lions (Laake et al., 2002; Tollit et al., 2007). Compounding the underreporting of large Pacific salmon is the possibility that bones from large salmon were not available in scat samples. Otariids are known to regurgitate and spew out bones from large fish (Gudmundson et al., 2006) and to not fully consume large fish, potentially reducing the availability of such bones to be identified (Tollit et al., 2017).

A second important caveat is the possibility that some of the juvenile Pacific salmon for which bones were examined in this study were consumed by another predator that was in turn eaten by a sea lion (Pierce and Boyle, 1991). Sea lions can target small-bodied prey, making it difficult to determine what portion of the bones of small Pacific salmon were from secondary consumption. Fiscus and Baines (1966) found 1280 capelin (*Mallotus villosus*) in the stomach of a juvenile Steller sea lion that had an average mass of 14.1 g, similar to the mass of juvenile Pacific salmon (Chasco et al., 2017a). For the third consideration regarding the results of this study, keep in mind that we analyzed only one bone from each size class of salmon for which bones were found in scat samples of California and Steller sea lions. This approach effectively required the assumption that California and Steller sea lions were eating only one species of Pacific salmon of a given size class during a meal. Roffe and Mate (1984) reported finding more than one species of salmon in sea lion gastrointestinal tracts, and given that result, we may not have detected all of the species of salmon present in each scat sample. Lastly, results from both captive feeding trials and studies in which genetic analysis was used for prey identification indicate that salmon bones are often not found in scat samples, even when sea lions are known to have consumed salmon (Tollit et al., 2003, 2017).

## Conclusions

California and Steller sea lions depend on Pacific salmon for a portion of their diets. This dependence can create conservation concerns for depleted runs of Pacific salmon and competition with fisheries given that populations of both species of sea lions in Washington are large and growing. It was not possible to quantify the effect of predation by California and Steller sea lions on populations of Pacific salmon in this study alone. Future studies will benefit from ecosystem modeling that incorporates data on the diets of

California and Steller sea lions from this study and from Scordino et al. (2022) to determine the effect of predation by both species of sea lions on populations of Pacific salmon.

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