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Estimates of Chinook salmon consumption in Washington State inland waters by four marine mammal predators from 1970 to 2015

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Abstract: Conflicts can arise when the recovery of one protected species limits the recovery of another through competition or predation. The recovery of many marine mammal populations on the west coast of the United States has been viewed as a success; however, within Puget Sound in Washington State, the increased abundance of three protected pinniped species may be adversely affecting the recovery of threatened Chinook salmon (*Oncorhynchus tshawytscha*) and endangered killer whales (*Orcinus orca*) within the region. Between 1970 and 2015, we estimate that the annual biomass of Chinook salmon consumed by pinnipeds has increased from 68 to 625 metric tons. Converting juvenile Chinook salmon into adult equivalents, we found that by 2015, pinnipeds consumed double that of resident killer whales and six times greater than the combined commercial and recreational catches. We demonstrate the importance of interspecific interactions when evaluating species recovery. As more protected species respond positively to recovery efforts, managers should attempt to evaluate tradeoffs between these recovery efforts and the unintended ecosystem consequences of predation and competition on other protected species.

Résumé : Des conflits peuvent survenir quand le rétablissement d'une espèce protégée limite le rétablissement d'une autre espèce protégée à cause de la concurrence ou de la prédation. Si le rétablissement de nombreuses populations de mammifères marins sur la côte Ouest des États-Unis est considéré comme une réussite, dans le Puget Sound de l'État de Washington, l'abondance accrue de trois espèces de pinnipèdes protégées pourrait avoir une incidence négative sur le rétablissement du saumon quinnat (*Oncoryhnchus tshawytchsa*), une espèce menacée, et de l'épaulard (*Orcinus orca*), une espèce en voie de disparition, dans cette région. Nous estimons que, de 1970 à 2015, la biomasse annuelle de saumons quinnats consommés par des pinnipèdes est passée de 68 à 625 tonnes métriques. En convertissant les saumons quinnats juvéniles en équivalents adultes, nous avons déterminé que, en date de 2015, les pinnipèdes en consommaient deux fois plus que les épaulards résidents, soient des quantités six fois plus grandes que les prises commerciales et récréatives combinées. Nous démontrons l'importance de tenir compte des interactions entre espèces dans l'évaluation du rétablissement d'espèces. Le nombre croissant d'espèces protégées réagissant positivement aux efforts de rétablissement fait en sorte que les gestionnaires doivent tenter d'évaluer les compromis entre ces efforts de rétablissement et les conséquences écosystémiques non voulues de la prédation et de la concurrence sur d'autres espèces protégées. [Traduit par la Rédaction]

Introduction

The recovery of many marine mammals around the world is a conservation success story (Magera et al. 2013), but it has also created new challenges for managing coastal ecosystems (Marshall et al. 2015; Smith et al. 2015). The often increasing abundances of marine mammals, and the associated potential for increasing consumption of fish and invertebrate prey, create the potential for conflicts between marine mammals and fisheries through competitive interactions. Therefore, adapting fishery stock assessment models and other natural resource management models to incorporate the effects of consumption by marine mammal predators may be needed to account for these trends and interactions in management decisions (Marshall et al. 2015).

Estimating predation mortality improves our understanding of predator–prey relationships and can inform fishery management reference points (Hollowed et al. 2000; Tyrrell et al. 2011). Until recently, many fisheries assessment models used around the world have ignored or made overly simplistic assumptions about trends in predation and other ecosystem processes that affect the productivity of commercially important fish stocks (Skern-Mauritzen et al. 2015). Some examples of well-documented marine mammal predation on harvested fish stocks include Cape fur seal (*Arctocephalus pusillus pusillus*) predation on hake (*Merluccius poli*) in South Africa (Punt and Butterworth 1995), consumption of Atlantic cod (*Gadus morhua*) by harp (*Pagophilus groenlandicus*) and grey (*Halichoerus grypus*) seals in eastern Canada (Mohn and Bowen 1996; Shelton et al.

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2006), consumption of herring (*Clupea harengus*) and forage fish by large whales in the northeastern United States (US) (Overholtz and Link 2007), harbor seal (*Phoca vitulina*) predation on Atlantic salmon (*Salmo salar*) in Scottish rivers (Butler et al. 2006), and consumption of salmon (*Oncorhynchus* spp.) and forage fishes by pinnipeds in the northwestern US (Wright et al. 2007; Thomas et al. 2011).

We focus here on marine mammal predation on Chinook salmon (*Oncorhynchus tshawytscha*), a culturally and ecologically important species of the northeastern Pacific. Chinook salmon are the largest of the Pacific salmon, and their anadromous life history connects freshwater and terrestrial ecosystems throughout the Pacific Rim (Hocking and Reynolds 2011). Chinook salmon serve as prey for top predators (e.g., Hanson et al. 2010) and contribute millions of dollars to both commercial and recreational salmon fishing (T.C.W. Economics 2008). However, many natural stocks of Chinook salmon in the contiguous US have been extirpated (Gustafson et al. 2007) or are at historically low levels and are protected under the US Endangered Species Act (Ford 2011). Chinook salmon biomass in much of the region has been maintained largely through the use of fish hatcheries, but even so, abundance remains well below historical levels (Naish et al. 2007). Causes for the decline of natural stocks include loss and degradation of freshwater spawning and rearing habitat, loss of habitat access due to hydropower dams and other blockages, historical overfishing, and interactions with artificially propagated fish (Ruckelshaus et al. 2002). In addition to marine mammals, other nonmarine mammal predators may be also limiting Chinook salmon recovery: aggregations of avian predators along the Columbia River are thought to consume 5–12 million Chinook salmon juveniles annually (Roby et al. 2003) and spiny dogfish that congregate near hatcheries in British Columbia are thought to consume between 0.5 and 7 million juvenile salmon annually (Beamish et al. 1992). Additional Chinook salmon predators include herring (Ito and Parker 1971) and salmon sharks (Nagasawa 1998). Quantifying the magnitude of marine mammal predation and putting this in the context of other factors impacting Chinook salmon is therefore becoming increasingly important.

The objective of our paper is to estimate temporal trends in both numbers and biomass of Chinook salmon consumed in the waters in and around Puget Sound, Washington, US, by four species of marine mammals (California sea lions (*Zalophus californianus*), Steller sea lions (*Eumetopias jubatus*), harbor seals (*Phoca vitulina*), and killer whales (*Orcinus orca*)). Fish-eating resident "killer" whales in the region, which are listed as Endangered in the US (the Southern Resident population), are highly specialized predators on salmon (Ford et al. 1998, 2016; Hanson et al. 2010), and previous authors have estimated the magnitude of this predation (Williams et al. 2011). However, harbor seals, Steller sea lions, and California sea lions also prey on Chinook salmon, and prey limitation has been identified as one of the biggest threats to resident killer whales (Ward et al. 2009). In particular, the inland waters of Washington State and British Columbia are thought to have one of the highest densities of harbor seals in the world, with abundance spurred by rapid population growth over the period 1970–2000 (Jeffries et al. 2003). The marine mammal species in the region differ in their foraging characteristics, such as reliance on Chinook salmon as prey, size of salmon they target, and the spatial and temporal distribution of foraging on salmon. Here, we develop a model to evaluate the relative importance of these four species as sources of mortality on Chinook salmon and to understand temporal trends in predation mortality. We are particularly interested in understanding whether competition for a shared prey resource may be an important factor limiting the population growth of endangered Southern Resident killer whales.

We focus our analysis on the Puget Sound region because the policy context is representative of many nearshore ecosystems (Marshall et al. 2015) and because this is a data-rich region (partic-ularly with respect to diet samples) that can serve as a case study to later expand to the broader US and Canadian West Coast. Our study region encompasses Puget Sound and nearby US waters, including the Strait of Juan de Fuca, Hood Canal, and the San Juan Islands. Both predators and prey in this area are federally protected and subject to ongoing recovery efforts. Chinook salmon from Puget Sound were listed as threatened under the US Endangered Species Act in 1999 (Federal Register 1999). Six years later, the Southern Resident killer whale population was listed as endangered, in part due to concerns about an adequate prey base (Federal Register 2005). Potential competitors with the killer whales include California sea lions, Steller sea lions, and harbor seals, which are all protected under the US Marine Mammal Protection Act. By developing a flexible bioenergetics and diet modeling framework, we hope to eventually see this framework expanded to evaluate trends in marine mammals and tradeoffs with Chinook salmon at a coast-wide level.

Methods

Although the Salish Sea consists of US and Canada waters, we focused our initial modeling efforts on the inland waters of Puget Sound and the surrounding areas (encompassing the Strait of Juan de Fuca, Hood Canal, and the San Juan Islands). The primary rationale for this constraint is that the temporal and spatial coverage of marine mammal surveys and marine mammal diet samples (e.g., scat samples) is more complete relative to other areas on the west coast. The bioenergetics model that we develop below consists of a set of nested equations that reflect the life history of the focal prey (Chinook salmon) and the level of specialization by the predators based on their age, sex, activity level, and presence within Washington State waters. The specific bioenergetics parameters for each predator species are based on published literature (Table 1). Rather than describe the details of the particular parameterization for each species-specific model, we provide general forms of the equations and refer the reader to the Appendix and the publicly available code illustrating detailed implementations of the model (https://github.com/bchasco/Inland, built by running the buildModel.r script for base case scenario and output for this paper). A full list of the variables and all model parameters is provided in Table 2.

Modeling energetic demands of the predators

Individual models for the energetic demands of the four predator species vary considerably between species (Table 3). We model basal metabolism based on the general Kleiber (1975) equation, which is a power function that depends on the body mass (M_b) of the predator:

$$(1) \qquad E = M_b^{\beta}$$

Depending on the species, this model of energetic demands may be disaggregated into different energy costs:

$$(2) \qquad E_{h,i,s,t} = \frac{P_{h,i,s,t} + GC_{h,i,s,t} + \sum_j AC_{h,j,i,s,t}}{Ef_{h,i,s,t}}$$

where the variable $P_{h,i,s,t}$ is the reproductive cost, $GC_{h,i,s,t}$ is the growth cost associated with an increase in body mass, $AC_{h,i,j,s,t}$ is the sum of all activity costs, and $Ef_{h,i,s,t}$ is the fraction of total energy not lost to digestive heat or excretion (for species-specific calculations of each variable, please refer to the Appendix Tables A1–A3 and Figs. A1 and A2, which provide the equations used in the paper). We allowed each of our four predator species (killer whales, harbor seals, California sea lions, and Steller sea

Table 1. List of references that were used to build the bioenergetics model.

Data	Harbor seals	Steller sea lions	California sea lions	Killer whales
Maximum age	Howard et al. 2013	Winship et al. 2001	R. DeLong, personal communication	25+
Weight-at-age	Pitcher and Calkins 1979; Boulva and McLaren 1979	Winship et al. 2001	Winship et al. 2006	Noren 2011
Maturity-at-age	Pitcher and Calkins 1979	Winship et al. 2002	Winship et al. 2002	
Sex and age ratios	Bigg 1969; Zier and Gaydos 2014	Winship et al. 2002	Winship et al. 2002; R. DeLong, personal communication	
Predator presence		Jeffries et al. 2014	Jeffries et al. 2014	Hauser et al. 2007
Predator abundance	Jeffries et al. 2003	Jeffries et al. 2014; Wiles 2015	Jeffries et al. 2014; NMFS 2015; R. DeLong, personal communication	Center for Whale Research 2016
Prey selectivity	Thomas et al. 2016	Thomas et al. 2016; Scordino et al. 2014	Thomas et al., in review; Scordino et al. 2014	Ford et al. 1998; Hanson et al. 2010
Energetic demands	Howard et al. 2013	Winship et al. 2002	Weise and Harvey 2008; Winship et al. 2002	Noren 2011

Table 2. List of subscripts, superscripts, variables, and parameters of the model.

Type	Name	Symbol
Subscript	Predator	h
	Predator age	i
	Chinook age	a
	Predator activity type	j
	Predator sex	s
	Day	t
	Year	y
Superscript	Chinook	Ch
	Inland waters	IW
Variable	Energetic demand	E
	Reproduction costs	P
	Growth costs	GC
	Activity costs	AC
	Lactation costs	LC
	Chinook energetic content	E^{Ch}
	Chinook consumed	C^{Ch}
	Predator abundance	N
	Predator weight	Wt
	Chinook length-at-age	$l(a)$
	Maturity	m
	Fecundity	F
Parameter	Predator age and sex proportions	p
	Fraction of predator population in inland waters	ψ
	Activity fraction	f
	Allometric constant for metabolism	α
	Allometric constant for metabolism	β
	Diet fraction	ϕ
	Age composition of Chinook in predator diet	ν

Table 3. Processes of the bioenergetics models by predator species where "×" denotes that the process is explicitly included in the energetic models: P, reproductive costs; GC, growth costs; Ef, metabolic efficiency; AC, activity costs.

Predator	P	GC	Ef	AC	Source
Harbor seal	×	×	×	×	Howard et al. 2013
Steller sea lion	×	×	×	×	Winship et al. 2002
California sea lion			×	×	Weise and Harvey 2008 Winship et al. 2002
Killer whale			×[a]	×	Noren 2011

Note: Parameter values and functional forms are detailed in Tables A1, A3, and A4.

[a]The daily prey energy requirements in Noren (2011) (eqs. 3 and 4) account for metabolic efficiency based on estimates from Williams et al. (2007).

whales, Howard et al. (2013) for harbor seals, Weise and Harvey (2008) for California sea lions, and Winship et al. (2002) for Steller sea lions. The energetic cost of a particular activity is a function of body mass ($M_{b,h,i,s}$) of predator h and the activity multiplier in a modified Kleiber equation (allowing for scaling of the basal metabolic rate):

$$(3) \qquad AC_{h,j,i,s,t} = f_{h,j,i,s,t} \times \alpha_{h,i,j,s} \times (M_{b,h,i,s})^{\beta_{h,j}}$$

The parameter $\beta_{h,j}$ has been set to 0.75 for killer whales (Noren 2011), California sea lions (Weise and Harvey 2008), and Steller sea lions (Winship et al. 2002); however, for harbor seals, the power parameter ranges between 0.76 and 0.87, depending on their activity state (Howard et al. 2013). The body mass for the predators was taken from life history tables or estimated based on growth models in the published literature (see Table 1 for references). Given their size and difficulty of collecting accurate killer whale body mass information, we address the effects of any uncertainty from this model input in our sensitivity analysis. Overall, the core energetic equations are eq. 2 for total energetic demand, combined with detailed representation of activity costs (eq. 3).

By modeling the body mass at age of the predators, our model retains the flexibility to track the impacts of individual predator cohorts. Bioenergetics models of pinnipeds often use coarser stages (e.g., pup, juvenile, and adult), so to map the stage-based parameters in the literature to our age-based models, we used information about maturity-at-age (Table 1). Parameters related to the pup stage were mapped directly to age zero ($i = 0$) individuals, such that $\theta_{i=0} = \theta^*_{pup}$ where θ^* is any stage-specific parameter in the literature. The maturity-at-age ogives in the literature (see reference in Table 1) suggest a continuous maturation schedule over several age-classes rather than the knife-edge maturity-at-age in

lions) to have unique parameter values related to basal metabolism (Table 3), but published estimates assume that reproductive and growth costs for California sea lions (Williams et al. 2007) and killer whales (Noren 2011) are sufficiently small and that the majority of the energetics costs are accounted for by the activity costs (i.e., the reproductive and growth costs are implicitly included in activity costs). Consistent with the published bioenergetics literature (Table 1), we assume that thermoregulatory costs are also implicitly included in activity costs.

The basal energy model (eq. 1) accounted for the age (i), activity (j), and sex (s) specific differences for a predator (h) throughout the year. Energetic costs are modeled on a daily time step (day t), and activities can be broken down into proportions of the total time engaged in each activity j ($f_{h,j,i,s,t}$) based on Noren (2011) for killer

the staged-based bioenergetics models. We assume that the parameters for individual animals older than age 0 were a weighted average of the juvenile ($\theta^*_{\text{juvenile}}$) and adult ($\theta^*_{\text{adult}}$) parameters based on the maturity-at-age (m_i):

$$(4) \qquad \theta_i = (1 - m_i)\theta^*_{\text{juvenile}} + m_i\theta^*_{\text{adult}}$$

The parameter estimates for age-classes with 100% juvenile or mature individuals will map identically to the stage-based estimate. For age-classes where the transition between juvenile and adult occurs, the age-specific parameter estimates will gradually begin to converge to the adult stage estimate.

Predator population dynamics, 1970–2015

The daily energetic demand of predator h, age i, and sex s is the product of the numbers-at-age ($N_{h,y}$) in year y (Appendix Fig. A2), the proportion of the animals in each age-class by sex and year ($p_{h,i,s,y}$), the fraction of the population present in inland waters on day t ($\psi_{h,t}$) (Appendix Fig. A3), and the daily energetic demands ($E_{h,i,s,t}$) (eq. 2):

$$(5) \qquad E_{h,i,s,t,y} = E_{h,i,s,t}N_{h,y}p_{h,i,s,y}\psi_{h,t}$$

For each of the predators in the model, we estimated the numbers-at-age from 1970 to 2015. The age, sex, and abundance of Southern Resident killer whales in inland waters were based on annual mark–recapture surveys with perfect detection probability (Center for Whale Research 2016), providing a complete census of the population since 1976 (although some neonate calves may have not been accounted for in the census). Time series of age and sex structure do not exist for pinnipeds, but there are estimates of stage-specific ratios for harbor seals (Howard et al. 2013) and estimates of sea lion age-specific mortality (Winship et al. 2002), from which we inferred a stable age distribution.

To generate estimates of harbor seal abundance, we used haul-out counts for the five population segments that make up the inland stock of harbor seals in Washington for the years 1978–1999 (Jeffries et al. 2003). Because these time series included missing values (particularly in later years), we fit univariate state-space models to the data from each population segment (Ward et al. 2010; Holmes et al. 2012) using the MARSS package in R (Holmes et al. 2012; R Core Development Team 2015):

$$(6) \qquad \log(N_{\text{HS},s,y+1}) = b_s \log(N_{\text{HS},s,y}) + r_s + v_{\text{HS},s,y}$$

$$(7) \qquad X_{\text{HS},s,y} = N_{\text{HS},s,y} \times e^{w_{\text{HS},y}}$$

Because they were conducted from the same aerial survey platform, we assumed that all five population segments had the same observation error variance (i.e., $w_{\text{HS},y} \sim N(0,\sigma_W)$, where $X_{\text{HS},s,y}$ is the observed survey abundance of population segment s and $N_{\text{HS},s,y}$ is the true population state. We allowed each time series to have unique trends (r_s), density dependence (b_s), and process variances ($v_{\text{HS},s,y} \sim N(0,\sigma_{v,s})$). The estimated states from each of the five population segments were then summed to create an abundance estimate for the total inland stock of harbor seals in Washington. The time series represent haul-outs only, so we have multiplied the estimates by 1.53 to account for individuals in the water (Huber et al. 2001). Because uncertainty exists in both the correction factor and harbor seal numbers (specifically, whether the population has been stable or declined slightly since 2000), we performed a sensitivity test to these assumptions. Although uncertainty in this correction factor exists (varying between 1.43 and 1.85 depending on regional location (Huber et al. 2001)), the linear properties of eq. 5 assume that any change in the correction factor results in a proportional change in the estimated consumption of

Chinook salmon by harbor seals. In other words, a 2% change in the correction factor translates to a 2% change in the estimated energy derived from Chinook salmon. To examine sensitivities to the assumption about a flat or gradual decline in harbor seal numbers over the last 15 years, we imposed a 4% decline consistent with other surveys (Pearson 2016, personal communication). Results from this scenario are included in the Appendix (Figs. A4 and A5). To determine the stable age distribution and sex ratio for harbor seals, we assume an initial 50/50 sex ratio for the pups and use stage-based mortality and fecundity estimates by Bigg (1969) to estimate the sex ratio for older ages.

Estimates of Steller sea lion abundance in inland waters are based on time series of haul-out surveys along the outer coast of Washington State from 1989 to 2015 (Wiles 2015) and aerial surveys of inland haul-outs during 2013 (Jeffries et al. 2014). Similar to harbor seals (eqs. 6 and 7), we estimated abundance for years with missing surveys using the univariate time series model in the MARSS package (assuming that inland and coastal trends in sea lion numbers are the same). This time series was then scaled to peak counts from inland waters (109 in 2013). To account for Steller sea lions that are not hauled out during the surveys, we applied a correction factor of 2 (National Marine Fisheries Service (NMFS) 1997). The sex and age ratio is based on age-specific survival estimates by Winship et al. (2002).

California sea lion abundance was based on relative population trends and point estimates of counts occurring in inland waters. To account for missing years in the California sea lion stock assessment (National Marine Fisheries Service (NMFS) 2015), we implemented a univariate state-space model similar to the one applied for harbor seals and Steller sea lions (eqs. 6 and 7). We assumed that the overall trend of California sea lions in Puget Sound was the same as the population trend of the entire stock, but we have little information for sea lion abundance within Puget Sound to scale the coast-wide estimate. There are minimum counts in inland waters in 1978 (no California sea lions were observed) and a peak abundance estimate of 1200 in 2005 (R. DeLong, NOAA MML, Seattle, Washington, personal communication, 2016), which we used to scale the coast-wide estimate. Finally, to account for seals that are not hauled out during the surveys, we again applied the correction factor of 2 (National Marine Fisheries Service (NMFS) 1997). The only California sea lions present in inland waters are nonpup males (Akmajian et al. 2014).

Because of availability of prey and behavior (e.g., breeding seasons), the fraction of each predator's population in inland waters ($\psi_{h,t}$) changes throughout the year. Harbor seals are the only predator that does not migrate outside the Puget Sound region ($\psi_{h,t} = 1, \forall t$). Killer whales have a seasonal presence in inland waters from May to November and are present infrequently and in small numbers during the winter months (Hauser et al. 2007; National Marine Fisheries Service (NMFS) 2008); additionally, studies suggest that even during the summer months, resident whales only occupy inland waters about 80% of the time. Based on continuous monitoring of haul-outs throughout the year, Steller sea lions have a bimodal distribution with a peak in early fall and winter and again in late spring through early summer, while California sea lions are only present from late fall through winter (Jeffries et al. 2014). The differences in abundance between surveys can be rather large, so to smooth the seasonal observations of sea lion presence by Jeffries et al. (2014), we averaged each abundance survey with the one before and after. To transform these average survey abundances to presence probabilities between 0 and 1, we divided each average abundance by the maximum average abundance.

Number of Chinook salmon consumed, 1970–2015

The number of Chinook salmon of age a that are consumed by predator h is a function of the daily energetic demands of the predator ($E_{h,i,s,y,t}$) (eq. 5), the fraction of predator's energy demand

Table 4. Length, energy content, and energy based on smolt equivalents for Chinook salmon with ocean ages from 0 to 5 within the Puget Sound inland waters.

	Smolt	Age 1	Age 2	Age 3	Age 4
Length (cm)	9.0	50	71	84	92
Energy (kJ)	54	12 280	36 694	62 028	82 400
Smolt equivalents	1	211	631	1067	1418

Table 5. Fraction and ocean age distribution of Chinook salmon in the diets of marine mammal predators in Puget Sound.

Predator	% diet	Chinook age composition (%)				
		Smolt	Age 1	Age 2	Age 3	Age 4
Harbor seal	6.8	31.0	17.0	17.0	17.0	17.0
Steller sea lion	6.4	31.0	17.0	17.0	17.0	17.0
California sea lion	6.1	16.0	21.0	21.0	21.0	21.0
Killer whale	51–95	0.0	2.0	18.0	55.0	25.0

derived from Chinook salmon ($\phi_{h,t}$), the proportion of the diet energy that is comprised of each age class of Chinook salmon ($\nu_{h,a}$), and the age-specific energetic content of the Chinook salmon (E_a^{Ch}):

$$(8) \qquad C_{h,s,a,y,t}^{Ch} = \frac{\nu_{h,a}\phi_{h,t}}{E_a^{Ch}} \sum_i E_{h,i,s,y,t}$$

This method assumes a single spatial box where the predator's ability to capture the Chinook salmon is not influenced by competition from other predators or the densities of the salmon within Puget Sound.

The fraction of prey species in the scat samples of predators is assumed to be proportional to the amount of energy derived from those prey species. Within Puget Sound, the diet fraction of Chinook salmon in resident killer whales has been estimated to range from 51% in the fall to 95% in the spring/summer based on observational studies and genetic analysis of scats (Ford et al. 1998; Hanson et al. 2010; Ford et al. 2016). The fraction of Chinook salmon in harbor seal diets is estimated to be 6.8% based on genetic analysis of scat samples, and that percentage can be disaggregated in to 2.1% juveniles and 4.7% adults based on hard parts such as bones and otoliths (Thomas et al. 2016). Steller and California sea lion diet data in Puget Sound are dominated by frequency of occurrence (FO) studies (Scordino et al. 2014), which only identify salmon to genus. Additionally, FO quantifies the fraction of times that prey were identified in a group of scat samples, which means the prey FO do not sum to 1 and are not representative of the diet fraction of prey (Tollit et al. 2015). Because the data collected by Thomas et al. (2016) for harbor seals have both aggregated genus-level information from FO data and the species-level information from genetic data, we estimated the Chinook salmon conversion factors between FO and genetic data to be equal to 0.25 for juveniles and 0.16 for adults. That is, for every 4% of juvenile salmon FO in a pinniped diet, there is 1% of juvenile Chinook salmon in the pinniped diet. After applying these conversion factors to the raw FO data collected by Scordino et al. (2014) for sea lions, the estimated Chinook salmon diet percentages are equal to 1.0% juveniles and 5.3% adults for California sea lions and 2.0% juveniles and 4.5% adults for Steller sea lions. This approach relies on the assumption that the relationship between salmon bone FO and Chinook salmon diet fraction is the same for all three pinniped species. Furthermore, evidence suggests that sea lion (Sigler et al. 2009) and harbor seal (Thomas et al. 2011) prey electivity changes in response to prey abundance. However, given the absence of independent surveys of prey diversity in inland waters and the temporal and spatial overlap of sea lions relative to harbor seals, we believe that harbor seal conversions from FO to diet composition are reasonable approximations for sea lions.

The energy content of the different ages of Chinook salmon was based on work by O'Neill et al. (2014):

$$(9) \qquad E_a^{Ch} = 0.000011 \times l(a)^{3.122} \times \frac{1000\ cal}{1\ kcal} \times \frac{4.184\ J}{1\ cal}$$

where, $l(a)$ is the average length-at-age for the Puget Sound populations (Table 4). The conversion of energy content to a common

currency (smolt equivalents) makes comparison possible across predators that target different-aged prey. For example, a 5 year old salmon (ocean age 4) that is 92 cm has the energetic equivalent of 1418 smolts (ocean age 0) that are 9.0 cm long (Table 4).

The rapid increase in energy content from smolt to age 1 can have major implications on the number of salmon consumed. To account for the growth of smolts during their time in inland waters, we used previously developed models to approximate juvenile Chinook salmon growth (Beauchamp and Duffy 2011). On average, hatchery smolts in Puget Sound are about 9.0 cm during their release in spring and reach about 14–15 cm by September. Over their first year, we allowed the length of the smolts to increase by about 2.5 cm a month, such that the smolts become ~40 cm juveniles by the following spring. By assuming only a single size at release, this model simplifies many of the stock-specific differences related to migration timing and juvenile life histories (i.e., yearling versus subyearling or hatchery versus wild) and treats all salmon in Washington State inland waters as originating from a single stock. To further simplify our model, we do not assume any intra-annual growth for salmon ages 1–4.

The distribution of the Chinook salmon age-classes in the predator diets ($\nu_{h,a}$) is based on diet studies by Ford et al. (1998) and Ford and Ellis (2006) for killer whales, Thomas et al. (2016) for harbor seals, and Wiles (2015) for Steller and California sea lions (Table 5). Killer whales feed almost exclusively on mature salmon and the age composition (based on years in the ocean) of Chinook salmon in their diet is 2% age 1, 18% age 2, 55% age 3, and 25% age 4 (Ford and Ellis 2006; Hanson et al. 2010). Based on scat samples, the composition of Chinook salmon consumed by pinnipeds is only described as juvenile or adult. Previous studies have estimated that approximately 31% of the Chinook salmon in the harbor seal diet is derived from juveniles (Thomas et al. 2016), while 31% and 16% of the diets for Steller and California sea lions, respectively, are juveniles (Scordino et al. 2014). Without additional information about the size of the adult Chinook salmon in the pinniped diets, we assume that the adult Chinook salmon diet fraction is distributed evenly across the four adult age-classes.

Chinook salmon population dynamics and movement

To quantify effects of smolt consumption on the future returns of mature fish, we adopted a simple forward projection model. This is a single stock model with annual time steps and is meant to act as a starting point for a future, more complex multistock Chinook projection model.

The annual consumption of smolts by the pinniped populations, $C_{y,0}^h$, is the sum across all days within a year ($\sum_s \sum_t C_{h,s,a=0,y,t}^{Ch}$), where h is the predator type. Comparing the effects of predation across predators with different preferences (smolts, adults) requires using a common currency and accounting for the survival between juvenile and adult stages. To compare these effects on the same scale, the adult equivalent of smolt consumption was estimated by subjecting smolts that would have been lost to predation to natural mortality and maturation. We did not assume that mortality was compensatory; fish that would have been lost to predation were subjected to the same natural mortality rates as fish that escaped predation. Survival and maturation are a function of the age-specific rates:

Table 6. Maximum daily energetic demands by sex for adult predators and the maximum daily number of juvenile (ocean age 0) and adult (integrated across all ocean ages 1–4) Chinook salmon that are consumed during the predator's period of peak occupancy.

Predator	Daily energy demands (kJ)		Juveniles consumed		Adults consumed	
	Male	Female	Male	Female	Male	Female
Harbor seal	14 908	14 807	5.32	5.37	0.02	0.02
Steller sea lion	177 163	104 621	2.09	1.24	0.25	0.15
California sea lion	95 408	36 091	0.26		0.14	
Killer whale	1 033 404	875 284			14.14	11.42

(10) $C_{y,a}^h = C_{y-1,a-1}^h \times \text{surv}_{a-1} \times (1 - r_a)$, for all $a > 0$

where surv_{a-1} is the survival from $a-1$ to a and r_a is the conditional probability of maturing at age a. The number of the adult Chinook salmon returning to inland waters (IW) is the number surviving up to year y times the conditional probability of returning at age a:

(11) $C_{y,a}^{\text{IW}} = \text{surv}_{a-1} \times r_a \times \sum_h C_{y-1,a-1}^h$

There are 21 distinct stocks of Chinook salmon in Puget Sound (Ward et al. 2015), each of them with varying levels of ocean survival and age composition (Myers et al. 1998). Coarse estimates of ocean mortality are from Argue (1983): the bimonthly instantaneous mortality rates were estimated as 0.035, 0.015, and 0.0075 for ocean ages 1, 2, and 3+, respectively. These translate into annual survival estimates of 0.43, 0.69, and 0.83, which are estimates of the aggregated sources of natural mortality and not attributable to any species-specific sources of mortality. While these estimates are lower than the Chinook Fishery and Assessment Model (Clemons et al. 2006), our goal was to roughly match the average age composition seen across stocks in Myers et al. (1998) prior to the large increases in the pinniped populations within Puget Sound and treat the Chinook salmon population in Puget Sound as a single stock. We assumed a single aggregate population with conditional probabilities of maturing at ocean ages 1, 2, 3, and 4 equal to 0.02, 0.45, 0.85, and 1.0, respectively. From these survival and proportion-at-age estimates, the average age distribution (by ocean ages 1–4) of adult fish returning to Puget Sound would be 0.05, 0.52, 0.37, and 0.06. These estimates are similar to the age composition of returning Puget Sound Chinook salmon averaged across stocks (Myers et al. 1998). For our forward projection model, we assumed that these ratios were constant for each cohort and year.

Sensitivity analysis

We evaluated the sensitivity of the bioenergetics model output to input parameters using the methods of individual parameter perturbation (IPP) and relative partial sums-of-squares (RPSS) as described in Bartell et al. (1986) and Harvey (2009). Although our model predicts consumption for the years 1970–2015, for simplicity the sensitivity analysis focused on numbers and biomass of Chinook salmon consumed in 2015, summed over all four predators. These methods test sensitivities of model output to model input CVs of 2%, 10%, and 20%. IPP measures the variance in the 2015 consumption estimates after perturbing a particular parameter, and the RPSS uses multiple linear regression to measure how much of the variance in the 2015 consumption estimates can be explained by a particular input relative to the variance explained by all inputs being examined. The sum across all of the RPSS for the different model inputs being tested is equal to the R^2. For either the IPP or the RPSS, larger values imply that the model is

more sensitive to a particular input. Several of the model inputs are not parameters but are a vector of outputs from previous studies, and in these cases, we treated deviations for a particular vector of model inputs as affecting all elements of the vector equally. For example, if the random deviate for killer whale mass were +10% for a particular simulation, the masses of all killer whale ages would increase by +10%. We tested model sensitivity to two attributes related to salmon: length when they enter the ocean (smolt length) and intercept for the condition factor (i.e., salmon condition, 0.000011 in eq. 9) and five attributes related to the pinnipeds: Kleiber multiplier (α), population abundance ($N_{h,y}$), fraction of Chinook salmon in the diet, composition of age 0 salmon in the diets, and pinniped mass-at-age. Because southern resident killer whales do not target age 0 smolts and their abundance is known without error, we only examined model sensitivity to their Kleiber multiplier, abundance, and mass-at-age.

Distinct from model sensitivity, there is also substantial uncertainty in key parameters and data sources, for instance, related to diet fractions, pinniped abundance, and bioenergetics parameters; in many cases, these uncertainties exceed the 20% CVs tested in systematic sensitivity tests such as IPP or RPSS. We therefore explored the predicted number and biomass of Chinook salmon consumed for all years, varying two-way combinations of the following model inputs, each by ±50%: (1) the length of the juvenile Chinook salmon between April and June, (2) the fraction of Chinook salmon smolts in the predator diets, (3) total pinniped abundance, and (4) predator activity multipliers (α in eq. 3). When changing the fraction of smolts in the predator diets, we assumed that the difference was applied evenly over the other Chinook salmon age-classes. For instance, a 50% decrease in harbor seal smolt fraction results in a 4% increase in the diet fractions of the other four Chinook salmon adult ages.

Results

Daily consumption rates

The daily energetic demands for male and female predators in Washington State inland waters ranged from 3539 kcal (1.48 × 10^4 kJ) for female harbor seals to 247 364 kcal (1.03 × 10^6 kJ) for male killer whales (Table 6). The peak period of occupancy within inland waters varies among predators (Fig. A3); thus, estimates of the average number of juvenile Chinook salmon consumed daily by pinnipeds is affected by the growth of Chinook salmon throughout the year. Based on their period of peak occupancy within inland waters, numbers consumed ranged from 0.24 individual fish for male California sea lions during the winter months to 5.4 smolts per day for male and female harbor seals during the spring and summer months (Table 6). The daily consumption of adult Chinook salmon (not including adult equivalents) across all predators ranged from 0.02 for male and female harbor seals to 14.1 for male killer whales. Consumption estimates for male predators of a given age were consistently higher than for females because of sexual dimorphism. Exceptions were that peak energetic demands of female harbor seals during lactation and pup

Fig. 1. Annual consumption of Chinook salmon in Puget Sound by numbers and metric tons by season for the four predator species. Seasons match those used within the FRAM model used for salmon management (Clemons et al. 2006). [Color online.]
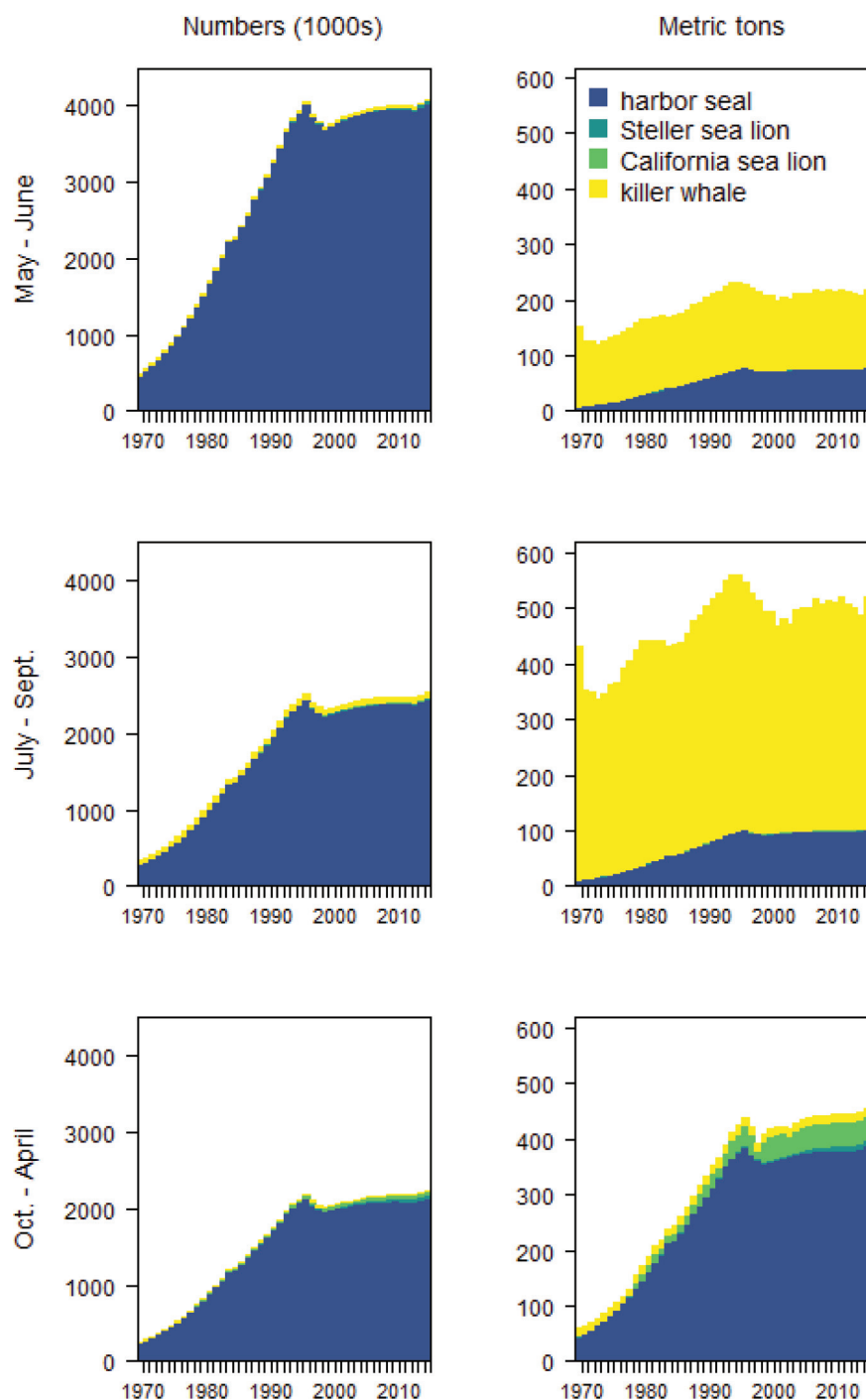

rearing were comparable to the peak energetic demands of the larger male harbor seals.

Comparing numbers to biomass consumed

The time series of Chinook salmon consumption by predators showed considerable differences depending on whether the unit of currency is numbers (Fig. 1, left) or biomass (Fig. 1, right). Summed across all seasons, beginning in 1970, harbor seals were estimated to consume a total of 1.1 million individual Chinook salmon, approximately 13 times greater in number than the 84 500 Chinook salmon consumed by killer whales that year. By 2015, the number of Chinook salmon consumed by harbor seals

was estimated to have increased to 8.6 million, or more than 104 times the 83 200 Chinook salmon estimated to be consumed by killer whales. One of our sensitivity tests included a scenario in which harbor seal populations declined by 4% annually after 1999 — this results in a decline in total harbor seal Chinook salmon consumption in 2015 to 4.1 million individuals (Appendix Fig. A5). In 2015, estimated consumption of numbers of Chinook salmon by Steller and California sea lions was closer to that of killer whales, with 104 000 and 55 700 individuals consumed, respectively. Because the killer whale population has remained relatively constant over the last 40 years, the estimated annual

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Fig. 2. Individual parameter perturbation sensitivity analysis of the (*a*, *c*, and *e*) numbers and (*b*, *d*, and *f*) biomass of Chinook salmon consumed in 2015 based on CVs of (*a* and *b*) 0.02, (*c* and *d*) 0.1, and (*e* and *f*) 0.2 for the parameters and variables in the model. The colored bar group parameters related to salmon growth (purple) and attributes related to harbor seals (dark blue), California sea lions (light blue), Steller sea lions (green), and killer whales (yellow). [Color online.]
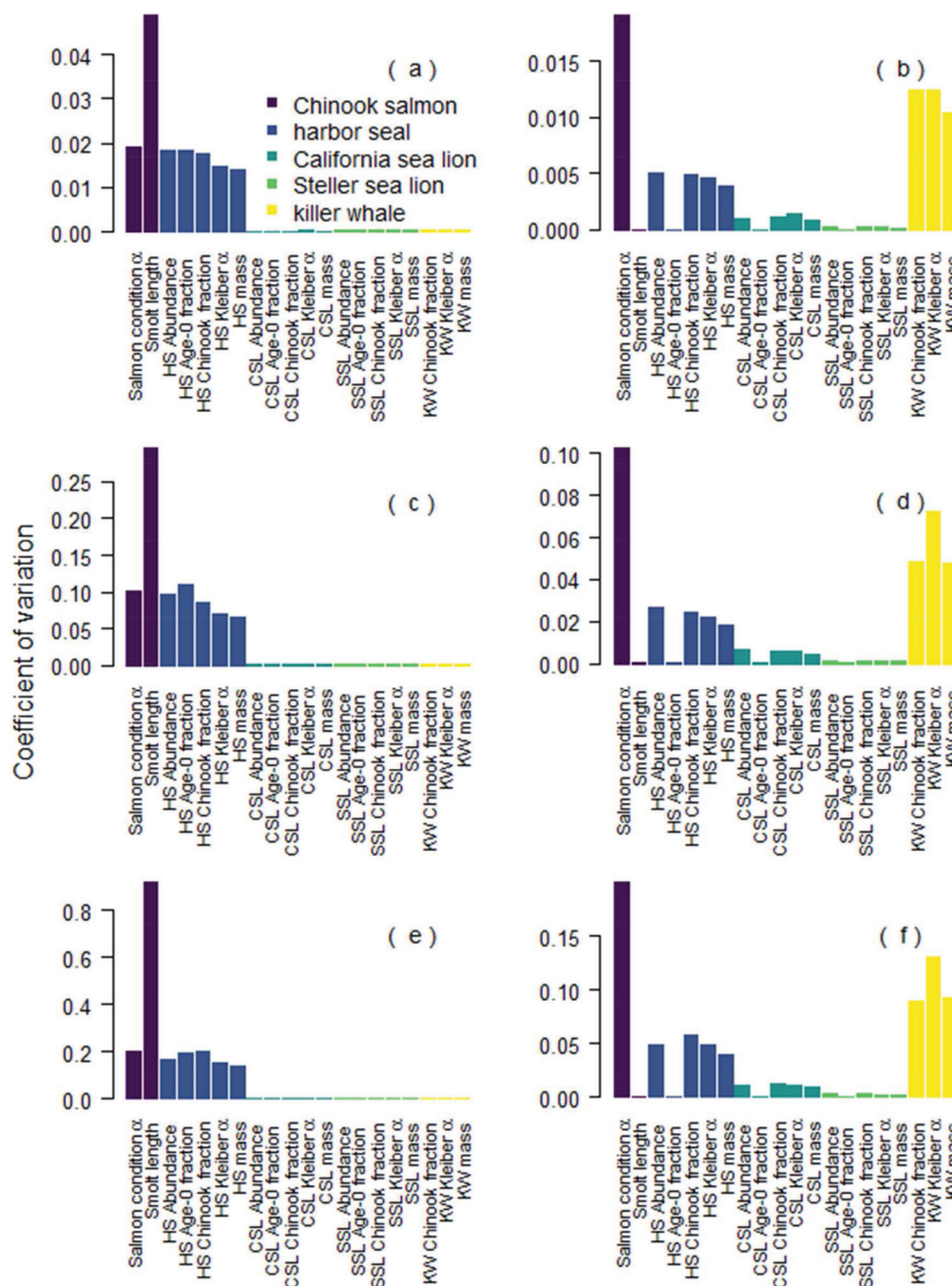
biomass of Chinook salmon consumed has also remained nearly constant, beginning with 576 metric tons (t) in 1970 and then decreasing to 567 t in 2015. Over this same time period, the estimated consumption by pinnipeds has increased from 68 to 625 t. The ratio of biomass consumed by killer whales to pinnipeds during the summer months (May through September when whales are most likely present) has decreased from 26:1 in 1970 to 3:1 by 2015.

In inland Washington State waters, killer whales are nearly absent during the late fall through winter months, and as a result, their consumption of Chinook salmon decreases from an average 554 t during spring and summer in 2015 to just 13 t during the fall and winter (Fig. 1). Conversely, sea lion abundance peaks during the fall and winter months (when killer whales are rarely present

in large numbers), and consequently, their consumption decreased from 54 t during fall and winter of 2015 to 3 t during spring and summer. Harbor seals are year-round residents, and their consumption of Chinook salmon is evenly distributed throughout the year, with between 38.0 and 55.0 t per month depending on their breeding/pupping activity.

Sensitivity analysis

The systematic IPP (Fig. 2) and RPSS (Fig. 3) sensitivity tests identified that model predictions of the numbers of Chinook salmon consumed in 2015 were most sensitive to smolt length, and the predictions of biomass consumed were most sensitive to the intercept for Chinook salmon condition factor (green bars in Fig. 2). Model predictions were more sensitive to parameterization

Fig. 3. Relative partial sums-of-squares sensitivity analysis of the (*a*, *c*, and *e*) numbers and (*b*, *d*, and *f*) biomass of Chinook salmon consumed in 2015 based on CVs of (*a* and *b*) 0.02, (*and d*) 0.1, and (*e* and *f*) 0.2 for the parameters and variables in the model. The colored bar group parameters related to salmon growth (purple), and attributes related to harbor seals (dark blue), California sea lions (light blue), Steller sea lions (green), and killer whales (yellow). [Color online.]
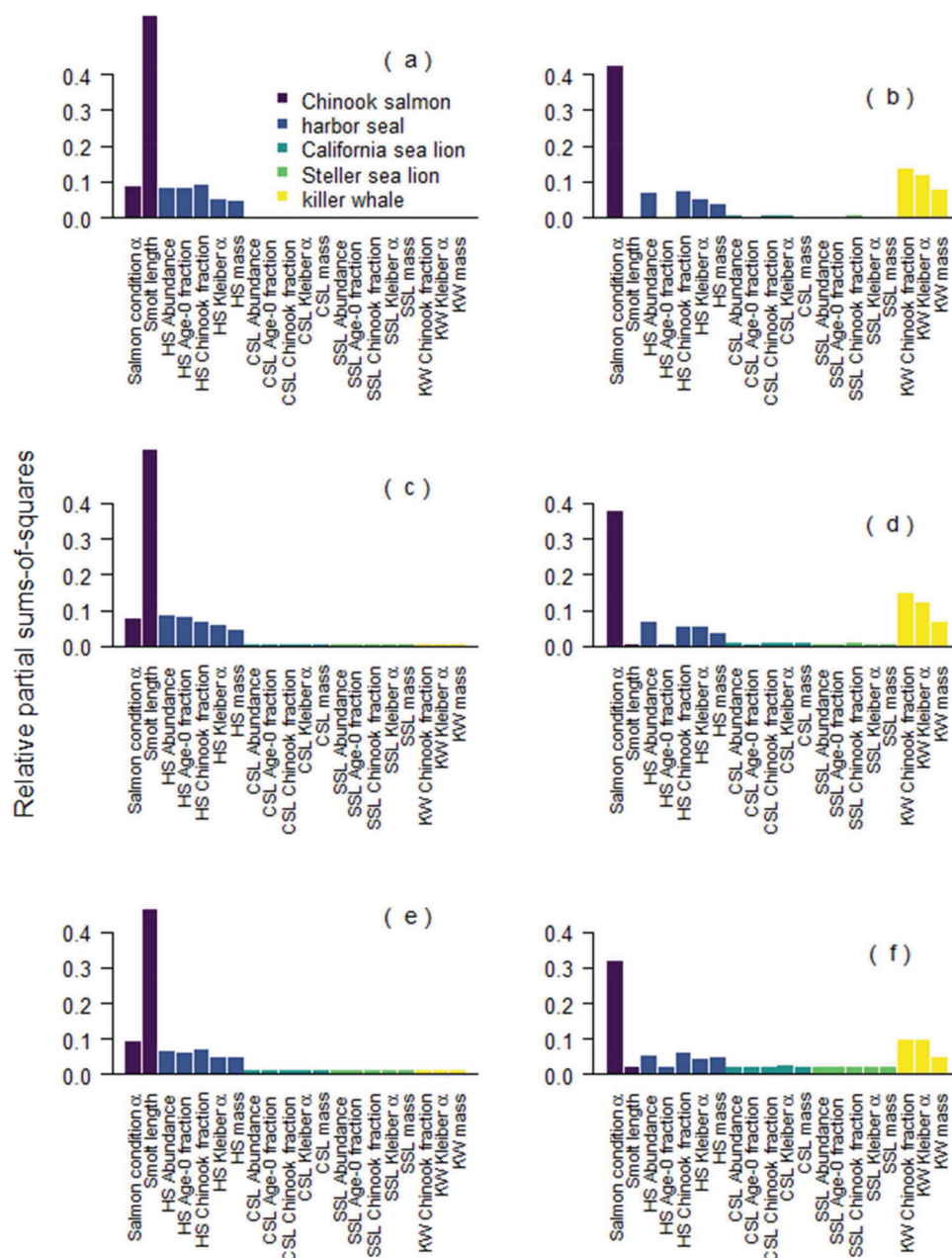
of harbor seals than they were to parameterization of other marine mammal predators. However, total biomass consumed responded substantially when parameters for killer whales had a high CV of 20% (yellow bars in Figs. 2 and 3).

The effects of uncertainty in key inputs and data are shown as a 3 × 3 contingency plot based on changes in the predator characteristics (Figs. A6 and A7) and Chinook salmon characteristics (Fig. A8). A 50% increase or decrease in either the predator activity multipliers or the predator abundance led to the same proportional changes in the biomass (Fig. A6) or number (Fig. A7) of Chinook salmon consumed. Conversely, there was a nonlinear response in the number of Chinook salmon consumed as a function of smolt length (Fig. A8); a 50% decrease in smolt length led to an ~300% increase in the number of Chinook salmon consumed

(left panels relative to middle panels in Fig. A8), whereas a 50% increase in smolt length led to a ~50% decrease in the number of Chinook salmon consumed (right panels relative to middle panels in Fig. A8). Similar to the changes in the predator abundance and predator activity, changes in the smolt fraction in the pinniped diets led to the same proportional change in the number of smolts consumed.

Pinniped effects on future returns

Between 1970 and 2015, most of the estimated increase in consumption on salmon resulted from pinniped predation on juvenile salmon smolts (Fig. 4). Smolt consumption for harbor seals was estimated to increase from 1.0 million in 1970 to a peak of 8.5 million in 2015, while consumption of adult Chinook salmon

Fig. 5. Number of juvenile Chinook salmon released by Puget Sound hatcheries (broken line) and the mortality as a function of the estimated harbor seal consumption (solid line), assuming that harbor seals in inland waters feed exclusively on Puget Sound hatchery Chinook salmon stocks.
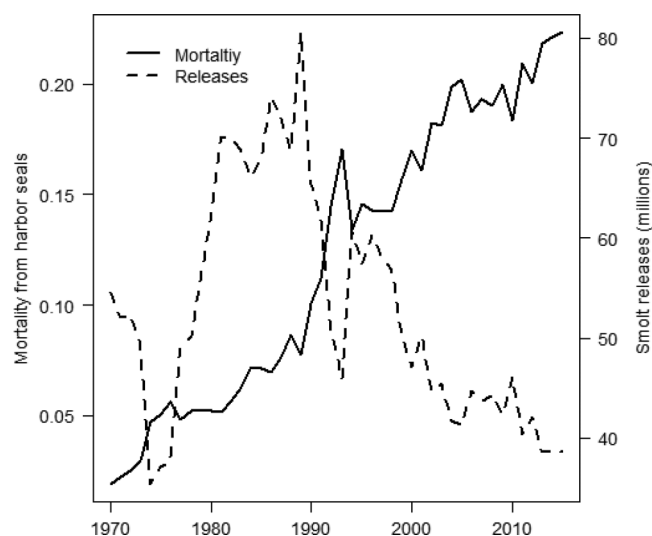
that pinnipeds — and in particular harbor seals — are a possible factor in this early marine mortality, as they prey on smolts.

Our bioenergetics modeling assumes that there is temporal and spatial overlap of harbor seals with outmigrating Chinook salmon smolts; however, seals do not feed exclusively in river mouths or estuaries (Orr et al. 2004, Lance et al. 2012; Luxa and Acevedo-Gutiérrez 2013) and the proportion of Chinook salmon in the diet can be highly variable (Thomas et al. 2016). When scaled up to the population level, the predicted daily consumption of Chinook salmon by an individual seal in our bioenergetics models is about 5.4 smolts per day during the spring outmigration. These estimates depend in part on harbor seal feeding behavior — individual seals may differ in their preference or encounter rate of smolts, with some individuals having a disproportionately larger impact on the population. Harbor seals alter their feeding behavior in response to seasonal pulses of other species like herring (Thomas et al. 2011), where FO of herring increases to about 40% during their spawning season. Following the pulse of herring spawning from February to April, harbor seals in inland waters may switch to wild and hatchery-released smolts (~40 million annually: PSIT (Puget Sound Indian Tribes) and WDFW (Washington Department of Fish and Wildlife) 2010) entering Puget Sound between May and July.

In addition to the mechanistic relationship between smolt mortality and pinniped bioenergetics, the decline in Salish Sea Chinook salmon marine survival (i.e., ~4.0% to <0.5% from the mid-1970s to the late 1990s, respectively: Quinn et al. 2005) coincides directly with the increase in the abundance of harbor seals. While several factors such as increasing temperatures in inland waters (Beamish et al. 2012), competition (Ruggerone and Goetz 2004), and changes in productivity (Mantua et al. 1997) have also been correlated with the declines, the scale and consistent abundance trend suggest that harbor seals should not be overlooked as potential contributors to declining marine survival. Assuming that Puget Sound Chinook salmon comprised 100% of the smolts in the diet of resident Puget Sound harbor seals (an overestimate, given that Chinook salmon smolts originating from British Columbia are also present in inland waters), we estimate that the annual consumption rate of just hatchery smolts (based on smolt release data from WDFW and PSTT (2004)) has increased from 1.8% in 1970 to 22.4% in 2015 (Fig. 5).

One of the strong assumptions made by our model is that Chinook mortality is additive (rather than compensatory), following the competing risks of death framework proposed by Hilborn et al. (2012). Compensatory mortality may arise when the mortality associated with one predator is replaced by another (consequently, altering the abundance of the first predator would have no impact on survival rates). In inland Washington waters, much of the Chinook mortality is thought to occur during early life stages. If harbor seals represent a major source of mortality for juvenile Chinook, and harbor seal numbers were to decline, it is unclear which other predators may increase their consumption of juvenile Chinook. Many avian predators, such as cormorants, have also declined in the region (Vilchis et al. 2015). Although compensatory mortality is difficult to quantify, future seal abundance surveys and Chinook returns may help us test these hypotheses.

The impacts of increasing pinniped abundance (and subsequent impacts on populations of fish prey) are not confined to just Chinook salmon. Many other potential pinniped prey are species of concern or listed under the US Endangered Species Act (herring, rockfishes (*Sebastes* spp.), steelhead (*Oncorhynchus mykiss*)) and may be affected by the increasing energetic demands of growing marine mammal populations (Ward et al. 2012). Additionally, these changing demands may also impact other top predators. Adult Chinook salmon are an important part of the Puget Sound commercial and recreational fishery, and they are also the preferred prey of endangered Southern Resident killer whales (Ford and Ellis 2006; Hanson et al. 2010; Ford et al. 2016). There is evidence to suggest that variation in birth and death rates of Southern Resident killer whales is linked to changes in Chinook salmon abundance (Ward et al. 2009; Ford et al. 2010). Our estimate of potential reductions to adult Chinook salmon abundance due to predation on smolts and subadults by pinnipeds (Fig. 4) could lead to reduction in the productivity or carrying capacity of Southern Resident killer whales. As a comparison, potential mortality from pinnipeds based on adult equivalents is comparable to commercial catches of Chinook salmon from Washington State inland waters, which have declined from approximately 250 000 adult salmon in 1980 to 100 000 in 2007, and recreational catches within Puget Sound have declined from approximately 150 000 to 50 000 (Puget Sound Indian Tribes (PSIT) and Washington Department of Fish and Wildlife (WDFW) 2010). Although our model is sensitive to assumptions regarding both marine mammals and Chinook salmon, the main results consistently suggest that across a broad range of parameter values, harbor seals and fish-eating "resident" killer whales account for the large majority of consumption of Chinook salmon biomass, and harbor seals consume many more Chinook salmon in terms of numbers of fish.

The ranking of harbor seals versus killer whale consumption of Chinook salmon biomass depends on uncertainty in pinniped abundance (killer whale abundance is known with high precision), but consistently across our scenarios, these two species had higher Chinook salmon consumption than did California or Steller sea lions. Our model is linearly sensitive to uncertainty in most parameters. For instance, estimates of biomass and numbers of Chinook salmon consumed (Fig. 1) depend on the predator diet fraction and size selectivity (eq. 8) (Figs. 2 and 3); therefore, changes in either of those parameters will lead to a proportional change in the consumption. Our results regarding numbers (but not biomass) of Chinook salmon consumed also depend upon assumptions regarding the ratio of juveniles and adults in the diets and the size of the juvenile Chinook salmon in inland waters. The parameterization of juvenile fish size can have a profound and nonlinear effect because the energy content of a fish increases with the cube of its length (eq. 9). If we reduce the smolt length at release from 95 to 45 mm (the difference between releasing fingerlings or fry), the energy content of a juvenile is reduced by ~90%, and therefore, the number of individual Chinook salmon

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needed to meet the energy demands of a predator is increased by a factor of 10. Similarly, the model is particularly sensitive to uncertainty in the fish condition (i.e., lean versus hig- lipid fish) and this can have impacts on both the biomass and numbers of salmon required to meet predator energetic demands (Figs. 2 and 3).

Based on bioenergetics modeling, the relative impacts of different marine mammal predators on Chinook salmon have changed substantially since the passage of the Marine Mammal Protection Act in 1972. Primarily due to increases in harbor seal abundance, since 1970, predation on Chinook salmon runs within Puget Sound has increased approximately ninefold in terms of numbers and doubled in terms of biomass. Large increases in harbor seal predation on smolts have potential impacts that are larger than either current commercial and recreational fisheries or predation by endangered Southern Resident killer whales. Sea lions also consume Chinook salmon; however, these impacts are estimated to be low compared to those from harbor seals. Our model only examines a subset of predators within Puget Sound inland waters and assumes that their Chinook salmon consumption is derived from only Puget Sound Chinook salmon stocks. Chinook salmon in inland waters are a mixture of US and Canadian stocks and it is likely that predators within these water do not feed exclusively on US stocks. It is also likely that the consumption by marine mammals along the salmon's migration route ranging from California to Alaska (Adams et al. 2016) is also impacting these US stocks. Further, there are other potential predators (harbor porpoise (*Phocoena phocoena*) and cormorants (*Phalacrocorax* spp.)) that are not included in our modeling efforts. We believe that this research is a valuable step toward decoupling the mechanisms that lead toward trends in marine survival in threatened Chinook salmon and provides a framework for coast-wide understanding of predation impacts on Chinook salmon and dependent predators such as Southern Resident killer whales.

Acknowledgements

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Appendix

Reproduction and growth costs for harbor seals and Steller sea lions

Reproduction costs

The daily production cost can be disaggregated into the gestation/pupping cost (PC) and lactation cost (LC). Depending on the time of year, the reproductive costs (PC and LC) will change for predators of different ages and sex. To account for these temporal effects, we include an additional set of time-varying estimates:

$$P_{h,i,s,t} = m_{h,i,s} \times F_{h,s} \times \left[PC_{h,i,s} \times \frac{p^{PC}_{h,s,t}}{\sum p^{PC}_{h,s,t}} + LC_{h,i,s} \times \frac{p^{LC}_{h,s,t}}{\sum p^{LC}_{h,s,t}} \right]$$

where the variables $p^{PC}_{h,s,t}$ and $p^{LC}_{h,s,t}$ are the conditional probability of predator p gestating or lactating on day t given that it is both mature ($m_{h,i,s}$) and fecund ($F_{h,s}$).

Since males neither lactate nor give birth, $F_{h,\text{male}}$ is equal to zero.

The lactation and gestation costs listed below are conditional on a female actually producing offspring. For harbor seals, the fecundity rate is 0.91 (Howard et al. 2013) and for Steller sea lions, the fecundity rate is 0.63 (Winship et al. 2002). For killer whales, gestation and lactation costs are implicitly assumed to be included within other modeled metabolic costs.

In most instances, the models in the literature (Table A2) describe the annual costs of reproduction. Since $p^{LC}_{h,s,t}$ and $p^{PC}_{h,s,t}$ are the daily probability of a reproduction cost, then $\frac{p^{LC}_{h,s,t}}{\Sigma t p^{LC}_{h,s,t}}$ and $\frac{p^{PC}_{h,s,t}}{\Sigma t p^{PC}_{h,s,t}}$ are the daily fraction of the annual reproduction costs. The killer whale literature does not separate the production costs from the activity costs, since at the population level, they are such a minimal cost compared to the activity costs. The gestation periods of the pinnipeds are based on the following: Tables A1 and A2 and Fig. A1.

Growth costs

The models for growth costs (GC) are different for each predator. The Steller sea lion model is an annual estimate based the change in body mass, while the harbor seal model is a daily estimate for immature individuals. The growth costs for killer whales are integrated into the activity costs (Table A3).

Efficiency

Efficiency measures the energy that is lost through excretion and digestive heat before it can be converted to maintenance or growth. Our estimate of efficiency (Ef) is the percent energy left after waste (d_a) and digestive heat (d_h) (Table A4). Calculating the conversion efficiency for each species is slightly different based on how the parameters were reported in the literature. Digestive efficiency for killer whales (84.7%) was accounted for in equations used to calculate daily prey energy requirements from field metabolic rates in Noren (2011).

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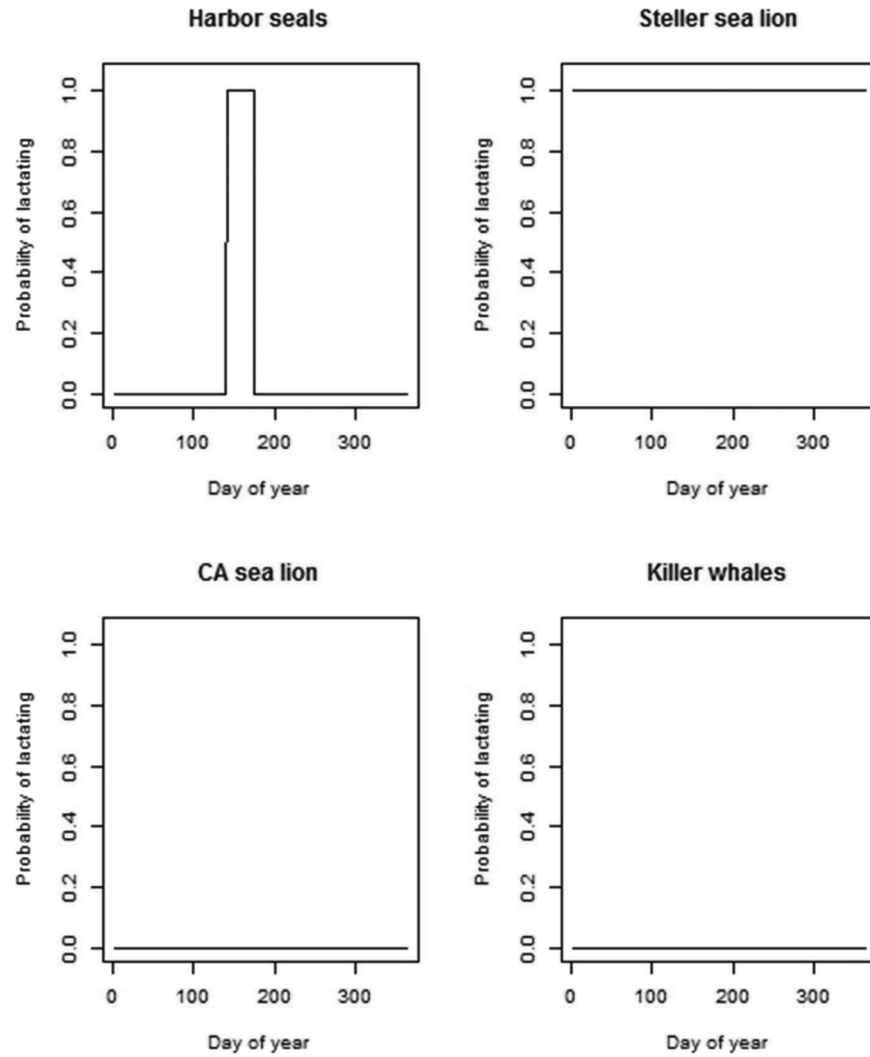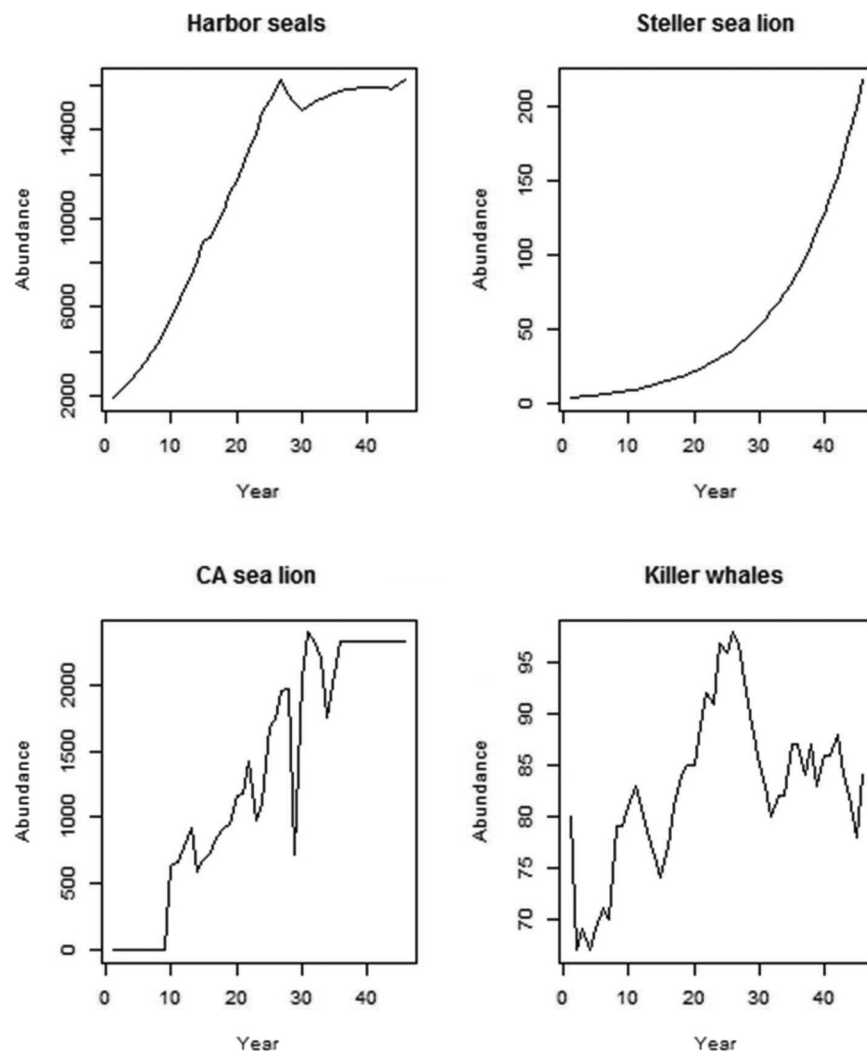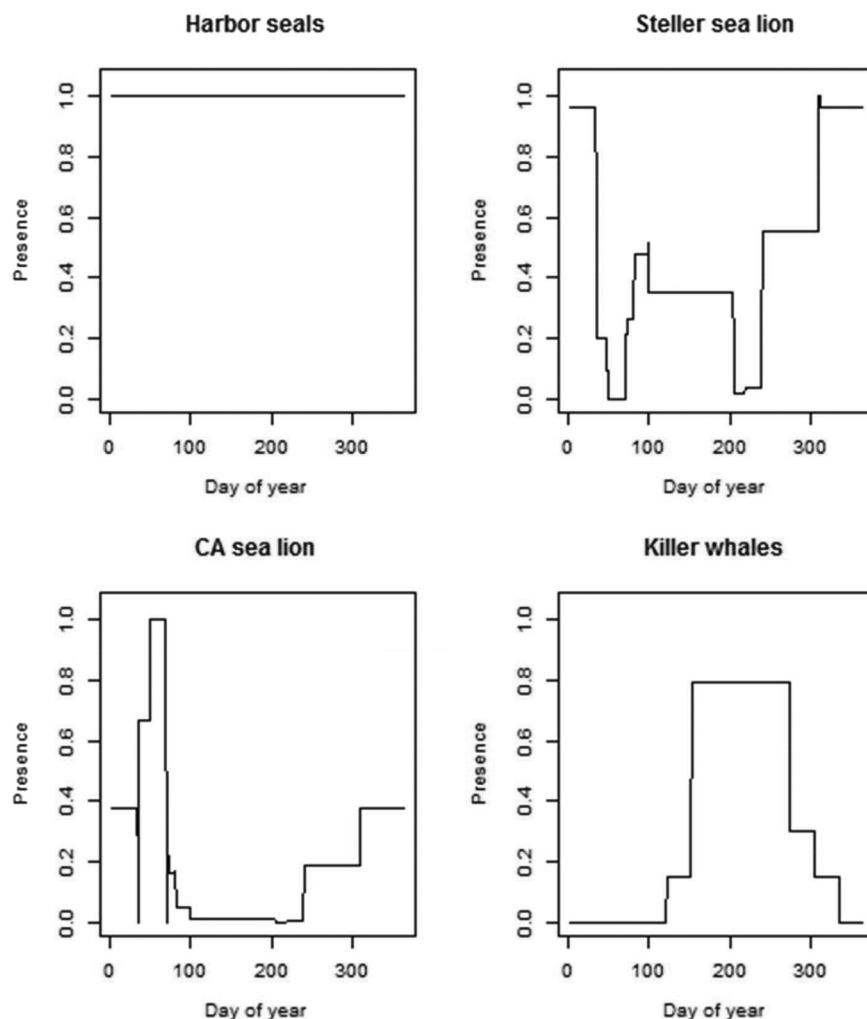
Fig. A1. Periods for which lactation costs are factored into the bioenergetics model.
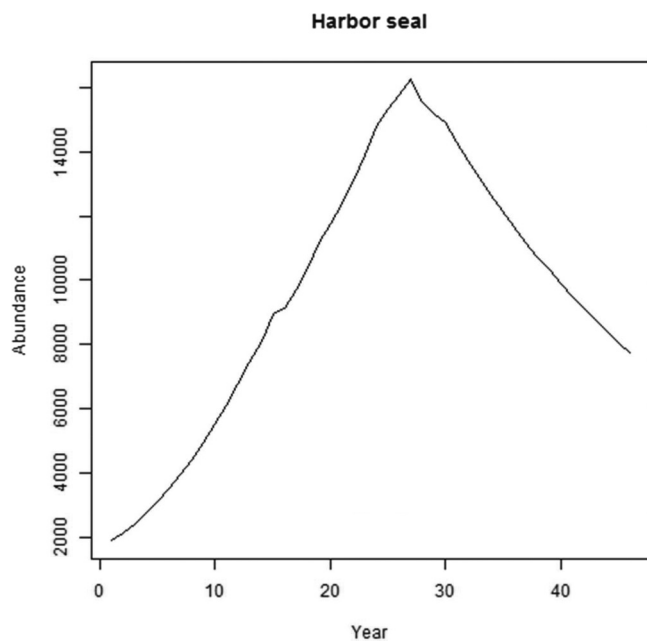
Fig. A2. Estimated annual predator abundance.

**Fig. A3.** Probability of the predators being present in inland waters.

Fig. A4. Population abundance of harbor seals, 1970–2015, in Puget Sound based on an annual 4% decline beginning in 1999.

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**Fig. A5.** Estimates of the annual consumption in numbers and biomass of Chinook salmon by marine mammal predators in Puget Sound between 1970 and 2015, assuming a 4% decline in harbor seal abundance beginning in 1999. [Color online.]
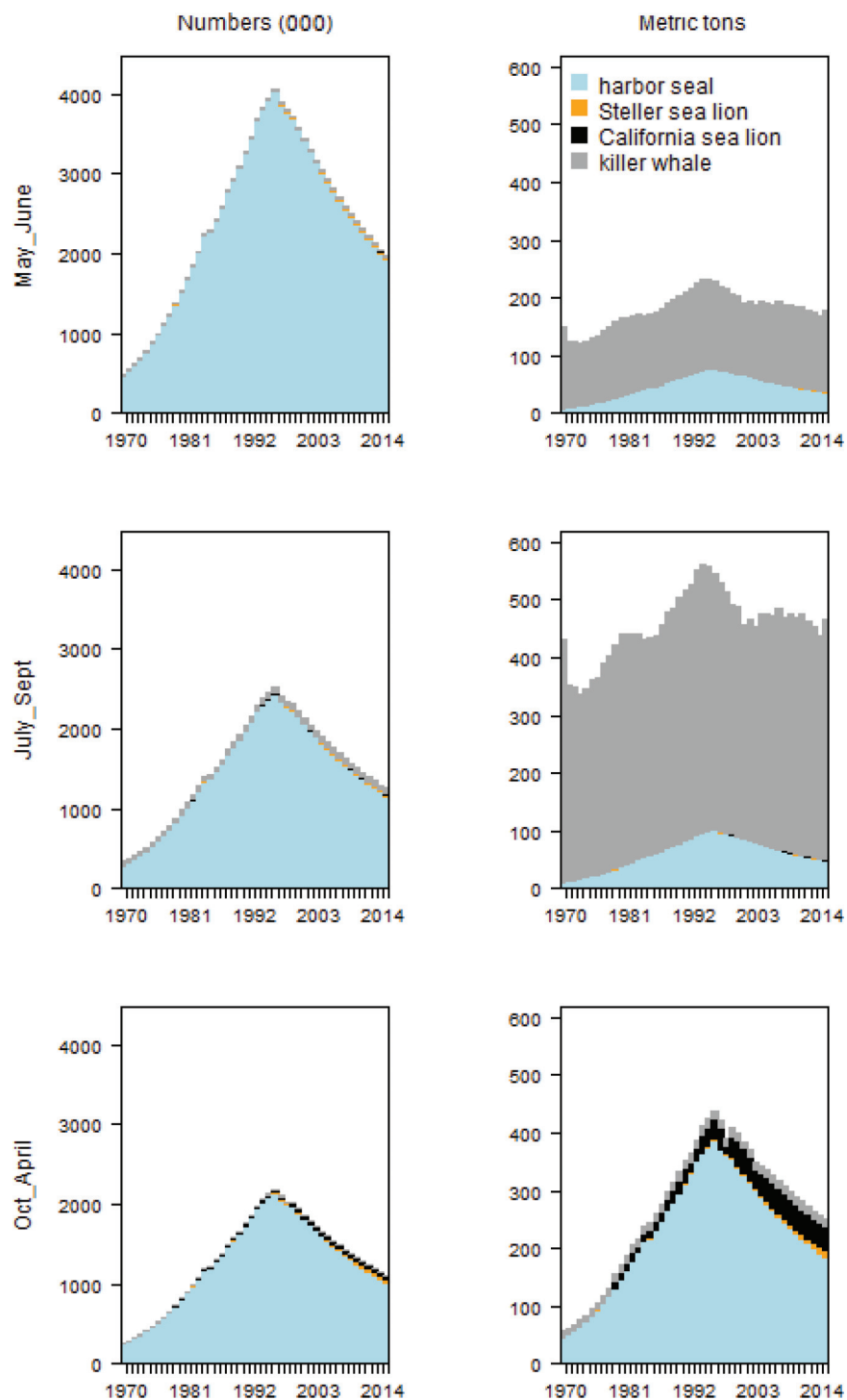
Fig. A6. Annual biomass of Chinook salmon consumed by each predator based on given combinations of pinniped abundance and predator activity. [Color online.]
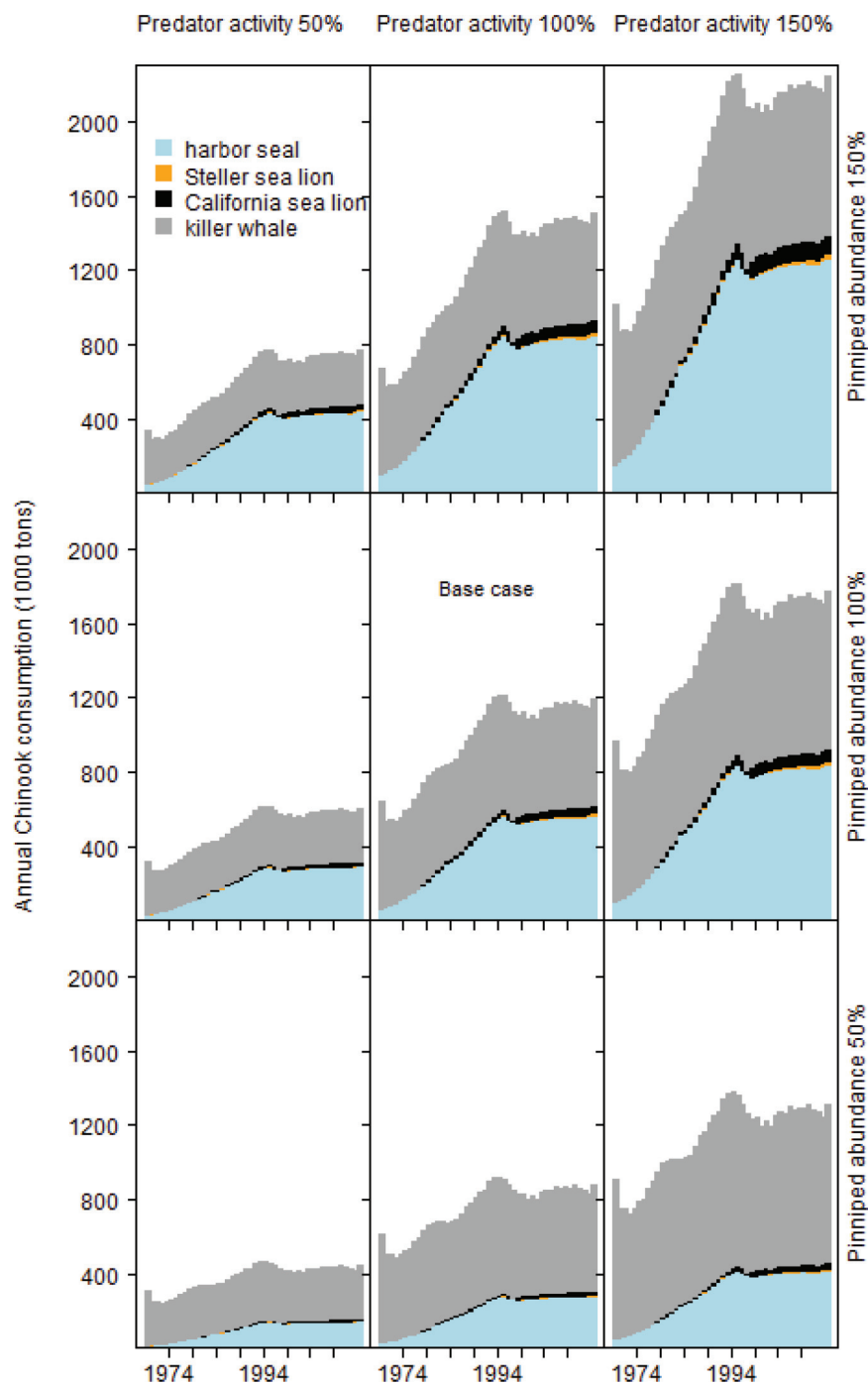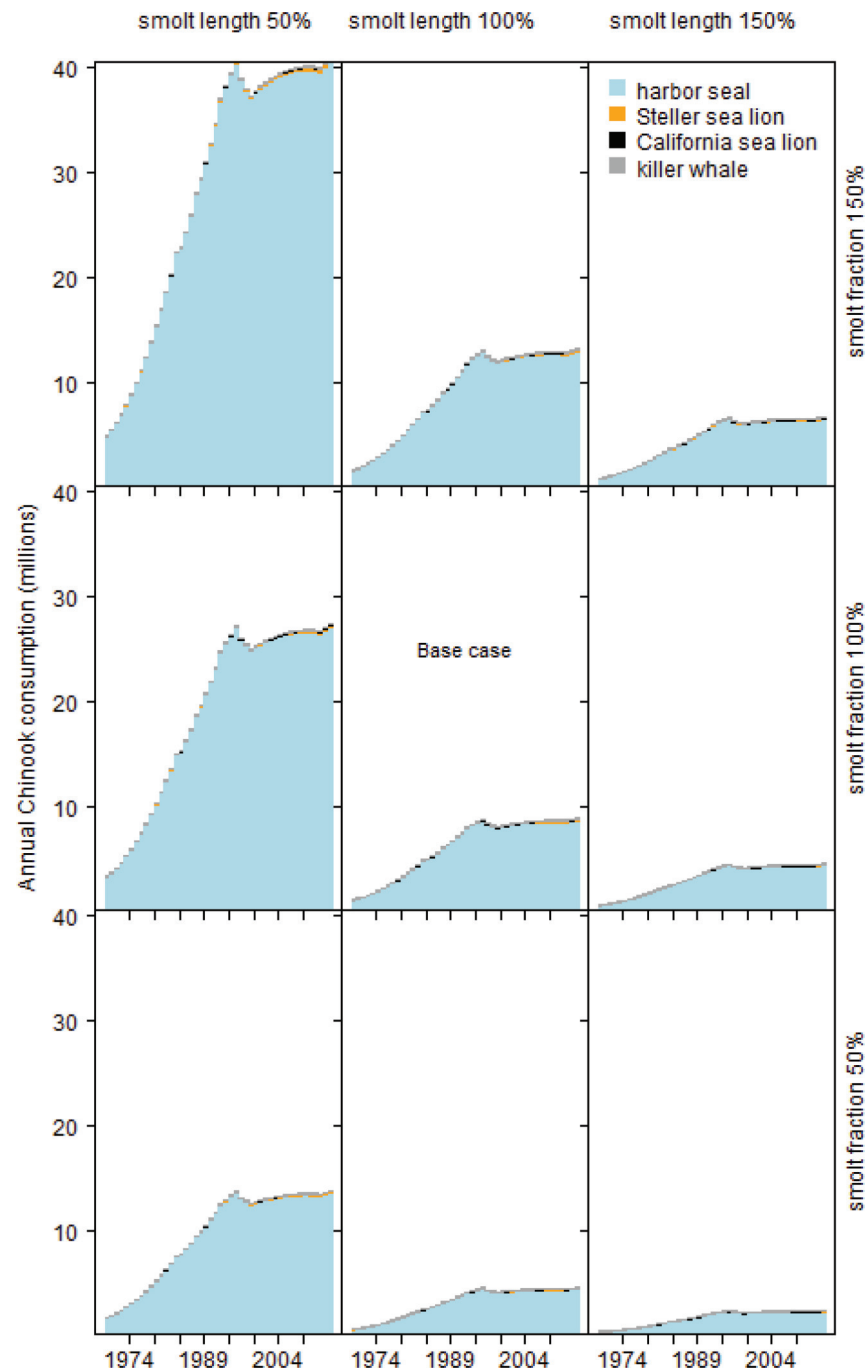
Fig. A7. Annual number of Chinook salmon consumed by the predators based on given combinations of pinniped abundance and predator activity. [Color online.]
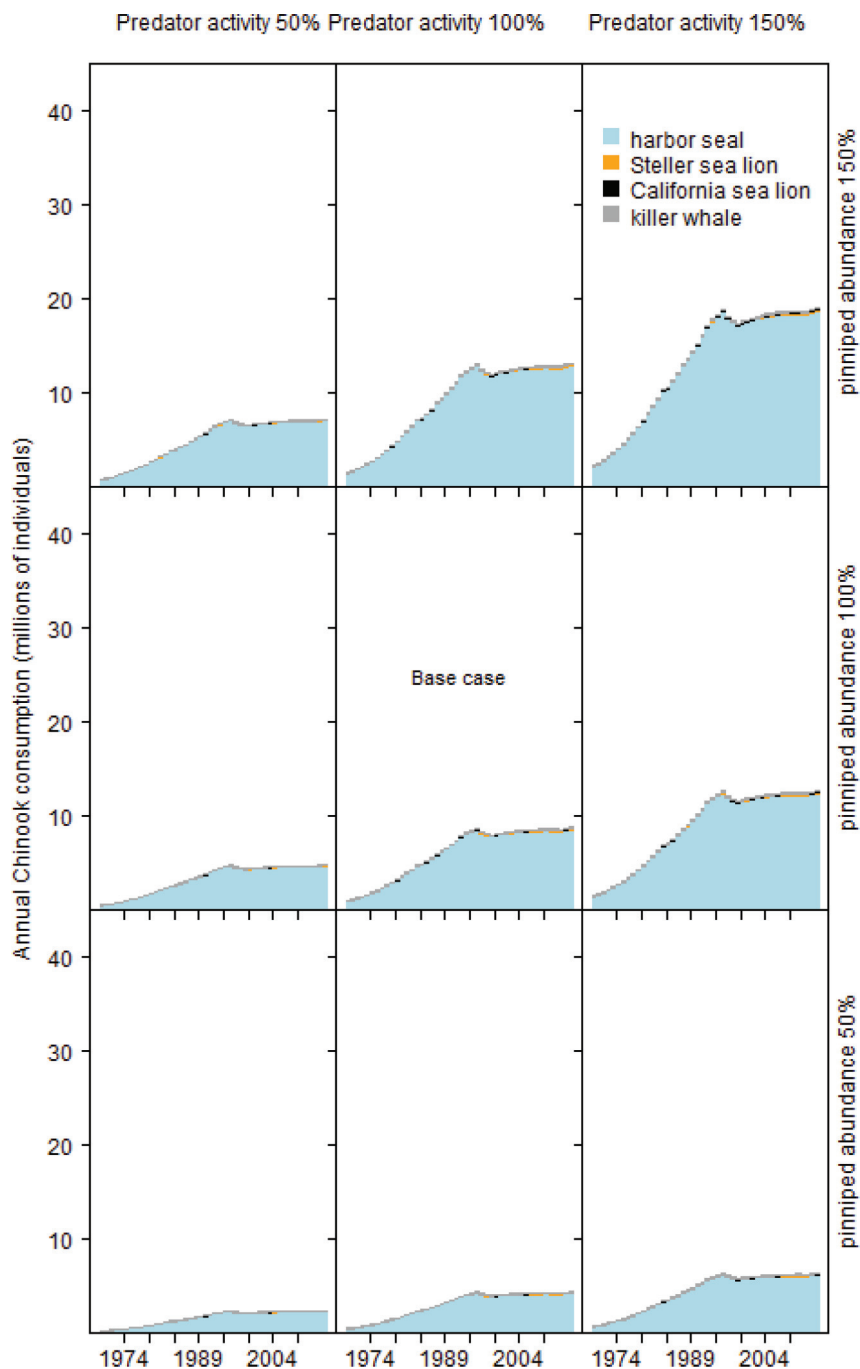
Fig. A8. Annual number of Chinook salmon consumed by the predators based on given combinations of smolt length and smolt fraction in the predator diets. [Color online.]

Table A1. Summary of reproduction costs by predator.

Variable	Predator	Model	Source
$PC_{h,i,s}$	Harbor seal	93 000 000 J/year	Howard et al. 2013
	Steller sea lion	$\mathrm{wt}_{h,i=0} \times [p_{\mathrm{lip}}\mathrm{ED}_{\mathrm{lip}} + (1 - p_{\mathrm{lip}})(1 - p_{\mathrm{w}})\mathrm{ED}_{\mathrm{pro}}] \times \dfrac{1}{d_{\mathrm{h}} \times d_{\mathrm{a}}}$ J/day	Winship et al. 2002
	California sea lion	Implicit[a]	Weise and Harvey 2008
	Killer whale	Implicit[a]	Noren 2011
$LC_{h,i,s}$	Harbor seal	$24\,000\,000 \times (\mathrm{wt}_{h,i,s})^{0.75}$ J/year	Howard et al. 2013
	Steller sea lion	$\dfrac{\sum a\mathrm{AC}_{\mathrm{a}}}{(d_{\mathrm{h}}-0.1) \times d_{\mathrm{a}}} - \dfrac{\sum a\mathrm{AC}_{\mathrm{a}}}{d_{\mathrm{h}} \times d_{\mathrm{a}}}$ J/day	Winship et al. 2002
	California sea lion	Implicit[a]	Weise and Harvey 2008
	Killer whale	Implicit[a]	Noren 2011
$p_{h,s}^{F}$	Harbor seal	0.91	Howard et al. 2013
	Steller sea lion	0.63	Winship et al. 2002
	California sea lion	Implicit[a]	
	Killer whale	Implicit[a]	

[a]The assumption is that these costs are implicit in bioenergetics models.

Table A2. Lactation and gestation periods for the each of the predator species.

Parameter	Predator	Initial day	N days	Source
$p_{h,i,s}^{\mathrm{PC}}$	Harbor seal	9 months before pupping	214 (9 months)	Temte 1991, 1994
	Steller sea lion[a]	9 months before pupping	214 (9 months)	Pitcher and Calkins 1981
$p_{h,i,s}^{\mathrm{LC}}$	Harbor seal	May 25	28–42	Muelbert et al. 2003
	Steller sea lion[a]	May	6 months	Mathisen and Lopp 1963

[a]Although some studies indicate that sea lions lactate for up to 9 months, many sea lions are seen lactating with 1–2 year old juveniles.

Table A3. Sources and model for determining growth costs for the predators.

Variable	Predator	Model	Source
$GC_{h,i,s}$	Harbor seal	$p_{i,s}^{m} \times 0.0165 \times 321 \times 86400$	Howard et al. 2013
	Steller sea lion	$(\mathrm{wt}_{h,i,s} - \mathrm{wt}_{h,i-1,s})[p_{\mathrm{lip}}\mathrm{ED}_{\mathrm{lip}} + (1 - p_{\mathrm{lip}})(1 - p_{\mathrm{w}})\mathrm{ED}_{\mathrm{pro}}]$	Winship et al. 2002
	California sea lion	Implicit[a]	Weise and Harvey 2008
	Killer whale	Implicit[a]	Noren 2011

[a]The assumption is that these costs are implicit in bioenergetics models.

Table A4. Efficiency calculations for the predator species.

Predator	Efficiency calculation	d_{a}	d_{h}	Source
Harbor seal	Ef = $d_{\mathrm{a}} - d_{\mathrm{h}}$	0.90	0.08	Howard et al. 2013
Steller sea lion	Ef = $d_{\mathrm{a}} \times d_{\mathrm{h}}$	(pup, others) 0.95, 0.85	0.88	Winship et al. 2002
California sea lion	Ef = $d_{\mathrm{a}} \times d_{\mathrm{h}}$	(pup, others) 0.95, 0.85	0.88	Winship et al. 2002
Killer whale	Ef = 0.847			Noren 2011