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ARTICLE

Quantifying impacts of harbor seal *Phoca vitulina* predation on juvenile Coho Salmon in the Strait of Georgia, British Columbia

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Abstract

Objective: Coho Salmon *Oncorhynchus kisutch* provide an important resource for recreational, commercial, and Indigenous fisheries in the Pacific Northwest. The goal of this study was to improve our understanding of how marine mammal predation may be impacting the survival and productivity of Coho Salmon in the Strait of Georgia, British Columbia. Specifically, we quantified the impact of harbor seal *Phoca vitulina* predation on juvenile Coho Salmon during their first several months at sea. Early marine survival is believed to be the limiting factor for the recovery of Coho Salmon populations in this region.

Methods: To estimate the number of juvenile Coho Salmon consumed by harbor seals, we developed a mathematical model that integrates predator diet data and salmon population and mortality dynamics.

Result: Our analysis estimated that harbor seals consumed an annual average of 46–59% of juvenile Coho Salmon between 2004–2016, providing the first quantitative estimate of seal predation in the Strait of Georgia.

Conclusion: Marine mammal predation on juvenile Coho Salmon is potentially a very important factor limiting survival and recovery of Coho Salmon in the Strait of Georgia.

KEYWORDS
Coho Salmon, DNA metabarcoding, harbor seal, predator–prey, Strait of Georgia

INTRODUCTION

Rapid increases in predator populations can alter ecosystem dynamics considerably, sometimes posing serious challenges to natural resource managers who are tasked with achieving multiple conservation objectives (DeMaster et al. 2001; Marshall et al. 2015; Smith et al. 2015). Often, a paucity of data can limit the ability to understand species interactions and may thwart efforts to identify tradeoffs or to evaluate competing alternative management strategies. In many cases, abundance time series are the only data available to infer relationships between predator and prey. Although correlative approaches are commonly used in ecology and fisheries to establish an association between predators and their prey (Worm and Myers 2003; Mäntyniemi et al. 2012; Tanasichuk and

Emmonds 2016), the strongest analyses demonstrate both a strong correlation and a credible mechanistic explanation (Hilborn 2016) that is supported by estimates of predator consumption rates.

Protection from hunting and culling has led to the recovery of many marine mammal populations throughout the world (Read and Wade 2000; Bowen and Lidgard 2013). Historically, culls or bounties on marine mammals were enacted to mitigate perceived impacts to valuable fish stocks, competition with fishers, damage inflicted to fishing gear, and depredation (Yodzis 2001; Trzcinski et al. 2006; Read 2008; Oliveira et al. 2020). Although some stakeholders regard recoveries of marine mammals as an unqualified conservation success story, the resulting ecological consequences of increased interactions between marine mammals and exploited or protected fish populations are often complex and unclear but potentially quite severe (Williams et al. 2011; Surma and Pitcher 2015; Walters et al. 2020).

Harbor seals *Phoca vitulina* experienced some of the most rapid population recoveries in the inland waters of the Salish Sea (Strait of Georgia, Puget Sound, and Strait of Juan de Fuca) following protection under the Fisheries Act (Canada) and the Marine Mammal Protection Act (United States) in 1970 (Jeffries et al. 2003; Olesiuk 2010). In the early 1970s, harbor seals in the Strait of Georgia numbered less than 5000 animals, whereas recent surveys suggest that the population is between 35,000 and 40,000 animals (Olesiuk 2010; Majewski and Ellis 2022). In addition, surveys in Washington State suggest that harbor seals in Puget Sound have exhibited a 7–10-fold increase in abundance since 1970 (Jeffries et al. 2003). Both populations are believed to be at or near the carrying capacity for the region. While the abundance of seals prior to hunting and culling was not known at the time, recent modeling efforts using contemporary abundance estimates and historical hunting data inferred that the population may have been lower than its current abundance, possibly due to hunting by Indigenous peoples (Nelson et al. 2023). Unsurprisingly, the observed trends in harbor seal abundances have prompted increased interest in the foraging ecology of these generalist predators (Thomas et al. 2011, 2022; Howard et al. 2013), especially since the abundances of valuable fishes like salmon and rockfish have declined severely over the same time period (Palsson et al. 2009).

Coho Salmon *Oncorhynchus kisutch* populations in the Salish Sea experienced drastic declines in abundance and productivity in the l970s and 1980s and have failed to recover despite marked reductions in fishing mortality rates since the 1990s (Preikshot et al. 2013; Zimmerman et al. 2015). Researchers have investigated a number of plausible biotic and abiotic explanations—for example, freshwater and marine habitat losses (Nehlsen et al. 1991; Magnusson and Hilborn 2003), overfishing (Rutter 1997), hatchery practices (Irvine et al. 2013), competition (Sobocinski et al. 2021), changes in ocean conditions (Coronado and Hilborn 1998; Mueter et al. 2005), changes in prey abundance (Beaugrand and Reid 2003; Ruzicka et al. 2011; Mackas et al. 2013), and even exposure to ultraviolet radiation (Melnychuk et al. 2012). Despite the considerable breadth and depth of research, only a handful of studies have attempted to quantify the impacts of predation on these populations of salmon in the Salish Sea (Beamish et al. 1992; Beamish and Neville 1995; Nelson et al. 2021).

Impact statement

Coho Salmon populations in the Strait of Georgia have experienced precipitous declines in marine survival over the last four decades. In this study, we used predator diet data to quantify the potential impact of harbor seals on juvenile Coho Salmon. Our results suggest seal predation may strongly influence survival of young salmon during their first several months at sea, and should be considered in future recovery efforts.

The failure of Coho Salmon populations in the Salish Sea to respond to reduced fishing mortality rates since the 1990s has led some to hypothesize that increases in natural mortality on juvenile fish due to predation by higher trophic levels, such as pinnipeds, may be preventing the recovery of some salmon and steelhead *O. mykiss* (anadromous Rainbow Trout) populations (Beamish et al. 1997; Sobocinski et al. 2020). Pinnipeds are often suspected of negatively impacting salmon populations because of their size, high energetic requirements, and tendency to interact with prey at the surface, where they are visible to people. Recent diet studies have also raised concerns that harbor seals may consume a major portion of the number of juvenile Coho Salmon residing in the Strait of Georgia, despite the fact that Coho Salmon make up a small portion of the overall harbor seal diet (usually <5%; Thomas et al. 2017, 2022). However, there has not yet been a similar effort to estimate the number of juvenile Coho Salmon that are consumed annually by seals, despite a strong negative association between Coho Salmon survival rates and seal abundance (Sobocinski et al. 2021). Thus, improved estimates of Coho Salmon that are lost to seal predation each year in the Strait of Georgia are important for identifying the most important factors affecting their abundance and productivity.

In this study, we estimated rates of seal predation on Coho Salmon by combining diet data from seal scats with a novel predation model that captures the bioenergetic demands of seals and the growth, survival, and abundance of juvenile salmon. We used this model to estimate current predation rates and changes in natural mortality rates since the 1970s; thus, we attempted to assess the potential for harbor seal predation on young salmon to have negatively affected the productivity of salmon populations in the Strait of Georgia. This study builds on previous research related to the impacts of seal predation on Coho Salmon and is the first study to attempt to quantify harbor seal consumption of Coho Salmon in the Strait of Georgia, which is critical to understanding how changes in predation rates may be affecting Coho Salmon population recovery.

METHODS

Study area

The Salish Sea is a large, inland body of water in the eastern Pacific Ocean, consisting of an intricate network of rocky fjords, shallow bays, and estuaries. The region is located between southwestern British Columbia, Canada, and the northwestern border of the United States in Washington State and consists of three main subregions: the Strait of Georgia, Puget Sound, and the Strait of Juan de Fuca (Figure 1). Its proximity to two major metropolitan areas—Vancouver, British Columbia, and Seattle, Washington—makes it a vital component of the fishing

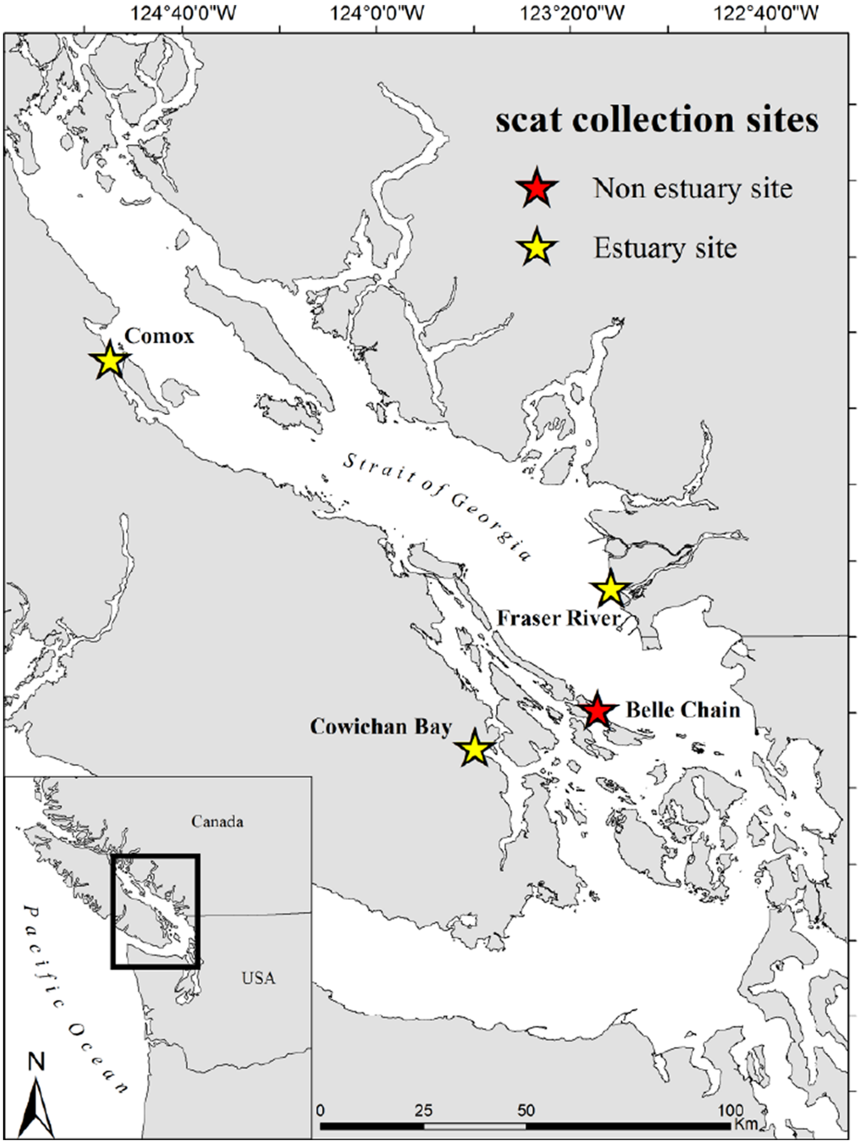

FIGURE 1 Locations of harbor seal haul-outs in the Strait of Georgia, British Columbia, Canada, where scat collections occurred. The four sites include three estuary haul-outs (Fraser River, Cowichan Bay, and Comox) and one non-estuary haul-out (Belle Chain). See Table 1 for a summary of the exact locations and sample sizes for each site.

industries in both countries; it serves as a fishing ground and a hub for fleets that target fish stocks throughout the North Pacific. The Salish Sea provides habitat for a multitude of commercially and recreationally important fish stocks, many of which have exhibited significant declines in catch and abundance since the mid-1980s (Harvey et al. 2012; Preikshot et al. 2013; Walters et al. 2020).

Predation model

We quantified the impact of seal predation on Coho Salmon by constructing a model that accounts for the abundance and prey requirements of the seal population in the Strait of Georgia and the abundance, growth, and natural mortality rates of juvenile salmon in their first year at sea. Using estimates of annual natural- and hatchery-origin smolt production in the Strait of Georgia, along with abundance estimates for the harbor seal population, we also inferred how predation rates may have changed over time. The model described here is predicated on the assumption that natural mortality of Coho Salmon can be modeled as a decaying power function of size—that is, natural mortality rates decrease as fish increase in size (Lorenzen 1996). Several studies have documented a strong relationship between body size and natural mortality of fish in both freshwater and marine environments and in both natural and captive settings (Lorenzen 1995, 1996, 2000). Further, it is well documented that the highest mortality rates experienced by juvenile salmon in the marine environment typically occur shortly after they enter marine waters (Parker 1968, 1971).

Model fitting

To estimate the mortality rates, numbers of individual fish consumed by harbor seals, and other quantities of interest, we used several parameter values available in the literature. Some of the parameters used in the model are well established from recent empirical studies (e.g., harbor seal abundance, daily energetic requirement), whereas others are uncertain or are not well studied. In particular, the allometric length exponent (c) and the instantaneous mortality rate (M^{Ref}) at the reference length (l^{Ref}) are difficult to estimate from the information available in the literature. The allometric length exponent is likely very close to 1.0 for Coho Salmon, but the only estimates available for the genus are for Rainbow Trout in captive (i.e., hatchery) studies (Lorenzen 2000). The M^{Ref} used in this study corresponds with the mortality rate of subadult Coho Salmon on their high-seas feeding grounds of the North Pacific (prior to fishing mortality) and their terminal migration through the Salish Sea, where they would encounter marine mammals (e.g., pinnipeds and killer whales *Orcinus orca*). Little is known about the mortality rates during this stage of the life cycle (Argue et al. 1983; Quinn 2018), but our model outputs are likely sensitive to their values.

We estimated the poorly known parameters M^{Ref} and c by fitting our predation models to 13 estimates of juvenile salmon abundance in the month of September, which were obtained from pelagic trawl surveys in the Strait of Georgia (Beamish et al. 2010; Boldt et al. 2019). We assumed that the deviations between the natural logarithms of the observed and model-predicted abundances were normally distributed, and we used the following objective function to fit the models:

$$L = \prod_{y=2004}^{2016} \frac{1}{N^{Obs}_{Sept,y}\sqrt{2\pi\sigma^2}} \exp\left\{ \frac{\left[\ln\left(N^{Obs}_{Sept,y}\right) - \ln\left(N_{Sept,y}\right)\right]^2}{2\sigma^2} \right\}, \quad (1)$$

where σ^2 is the variance on the logarithmic scale and is equal to $\ln(CV^2 + 1)$, with CV being the coefficient of variation; $N^{Obs}_{Sept,y}$ is the observed abundance; and $N_{Sept,y}$ is the model-predicted abundance. The CV of the abundance data from trawl surveys was assumed to be 0.30, which was the mean of four published surveys conducted between 2004 and 2007 (Beamish et al. 2010). Function minimization and all other quantitative analyses were performed in R (R Core Team. 2017), and the negative log-likelihood, $-\ln(L)$, was minimized using the "optim" function with the BFGS algorithm.

Salmon abundance data

Calculating the Coho Salmon mortality/predation rates required annual estimates of total juvenile production (i.e., the total number "at risk") from both natural and hatchery populations. For this analysis, we only considered natural and hatchery populations of Coho Salmon that originated from streams and rivers within the Strait of Georgia (Figure 1). Although juvenile Coho Salmon move among basins in the Salish Sea throughout the spring and summer (Beacham et al. 2016), the goal here was to estimate predation rates only for the Strait of Georgia.

Annual hatchery production was calculated by collating publicly available release records from the Regional Mark Information System database (www.rmpc.org; accessed June 1, 2019). In the Strait of Georgia basin, hatchery releases of Coho Salmon average between 5 and 10 million fish/year (Figure 2; Appendix Table A.3). It is important to acknowledge that not all hatchery-released fish survive to reach the marine environment, where they are fully vulnerable to predation by seals, even though seal predation can occur in the riverine environment (Olesiuk et al. 1995). Downstream/freshwater survival rates from release to salt water are likely to vary considerably by watershed and probably average between 50% and 90% (Bradford 1995; Quinn 2018). Based on existing studies, we assumed that the freshwater survival rates were 70% for Coho Salmon (Melnychuk 2009). We estimated the total number of juveniles entering the Strait of Georgia each year (y) as

$$N_{0y} = \gamma N_y^{Natural} + \gamma N_y^{Hatchery}, \tag{2}$$

where γ is the freshwater/downstream survival rate and N_{0y} is the initial number of fish in year y. The hatchery component of the population is known from stocking records, and the natural component was estimated as indicated in the next paragraph, with a calculation that included a natural mortality rate for downstream migration prior to ocean entry.

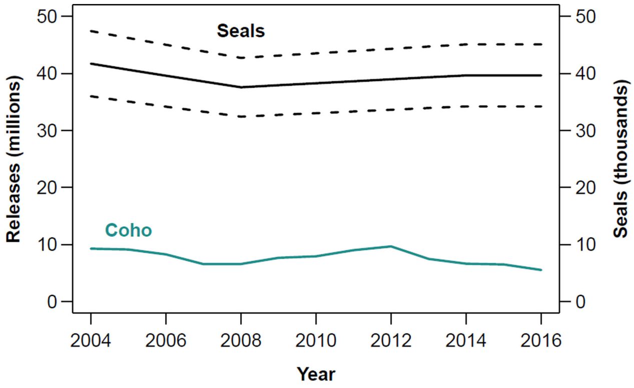

FIGURE 2 Annual harbor seal abundance (black line) and hatchery releases of Coho Salmon (teal line) in the Strait of Georgia. Black dashed lines are the 95% confidence intervals around the estimates of seal abundance, assuming a coefficient of variation of 0.07 (Olesiuk 2010). Annual hatchery releases of Coho Salmon were calculated from entries in the Regional Mark Information System database (www.rmpc.org; accessed June 2019).

Estimating ocean entry numbers of natural-origin Coho Salmon was less straightforward than the estimation for hatchery-origin salmon, as there are no public or private records of the hundreds of individual streams that produce juvenile Coho Salmon in the Strait of Georgia basin. Accordingly, we depended on existing studies that estimated recent juvenile production in the region to serve as inputs into our model. We used an estimate of annual smolt production from an existing model that employed the predictive distribution of the number of smolts produced per spawner from a Bayesian hierarchical model to extrapolate to the entire Strait of Georgia based on total available habitat (Korman and Tompkins 2014). The study concluded that average production of natural-origin Coho Salmon smolts had not changed significantly since the 1970s.

Harbor seal abundance data

A time series of harbor seal abundances in the Strait of Georgia is available from Fisheries and Oceans Canada's published aerial surveys in British Columbia (Olesiuk 2010). Actual count data are not available every year—rather, they are typically available every 2–3 years—so we used model-estimated abundances from a previous study wherein a state-space model was fitted to the aerial survey data (see Nelson et al. 2019b; Figure 2; Table A.3).

Harbor seal diet data

Harbor seal scat samples were collected from haul-outs at four different locations in the Strait of Georgia, British Columbia (Figure 1; Table 1), between April and December from 2012 to 2014. A detailed description of scat collection protocols is available from Thomas et al. (2017) and Voelker et al. (2020). Essentially, this data set consists of the samples from the Thomas et al. (2017) study in addition to 288 samples that were collected in Cowichan Bay between April and December of 2014 (Figure 1; Table 1).

TABLE 1 Summary of harbor seal scat collection data from four sites in the Strait of Georgia. For each collection site (locations shown in Figure 1), the location, total sample size, collection years, and collection months are shown, along with the source of the data.

Site	Latitude, longitude	Sample size	Collection years	Collection months	Source
Cowichan Bay	48°44′14.28″N, 123°37′17.76″W	595	2012–2014	Apr–Dec	Thomas et al. 2017; Voelker et al. 2020
Comox	49°35′45.53″N, 124°52′4.39″W	395	2012–2013	Apr–Nov	Thomas et al. 2017
Fraser River delta	49°4′27.17″N, 123°8′49.46″W	311	2012–2013	Apr–Oct	Thomas et al. 2017
Belle Chain	48°58′10.73″N, 123°29′34.63″W	183	2012–2013	Apr–Oct	Thomas et al. 2017

We combined the diagnostic hard structures (e.g., otoliths and bones) with DNA extracted from each scat sample to estimate the proportion of salmonids (by species) in the seal diet using the DNA metabarcoding approach of Thomas et al. (2017). This method integrates separate analyses of hard parts and DNA through an algorithm that apportions the salmonid DNA component in each sample to a "juvenile" or "adult" classification. The decision algorithm is based on (1) the presence/absence and/or co-occurrence of juvenile and adult hard parts with DNA and (2) known seasonal life history information. We used the resulting diet sample proportions to calculate monthly averages for each prey species and then used a simple moving average calculation (period = 4) to smooth the monthly estimates and thereby create a weekly time series for input into the predation model (Table 2).

Predation model formulation

In each year y, an initial cohort of out-migrating smolts leaving freshwater in the spring (N_{0y}) is subjected to a total natural mortality rate, which is the sum of mortality from harbor seal predation (M_t^{Seal}) and all other sources (M_t^{Other}). The model was projected forward from the beginning of the spring out-migration in the first week of April on a weekly time step (t) for a full year ($t = 1, \ldots, T$; $T = 52$):

$$N_{t+1,y} = N_{t,y} \exp\left[\left(-M_t^{Other} - M_{t,y}^{Seal}\right)t\right]. \tag{3}$$

Non-seal mortality M_t^{Other} is a function predicted from a "reference" mortality rate at the asymptotic length relative to their current size (see Lorenzen 1996, 2000):

TABLE 2 Monthly mean proportions of juvenile Coho Salmon in the harbor seal diet. Diet proportions are based on 1484 scat samples collected from four haul-out sites between April and December of 2012–2014.

Month	Sample size	Diet proportion
Apr	74	0.048[a]
May	158	0.005
Jun	152	0.026
Jul	178	0.038
Aug	189	0.009
Sep	336	0.001
Oct	303	0.006
Nov	83	0.000
Dec	11	0.000

[a] Diet proportions for Coho Salmon in the first 3 weeks of April were set to zero, as out-migrating Coho Salmon likely do not reach the ocean until late April at the earliest.

$$M_t^{Other} = \frac{M^{Ref}\left(\frac{l^{Ref}}{l_t}\right)^c}{T}, \tag{4}$$

where M^{Ref} is the instantaneous natural mortality rate at the reference length l^{Ref}; l_t is the length in week t, which is the length from the previous week plus a weekly growth increment ($l_{t+1} = l_t + [g/4.35]$) that is constant (Argue et al. 1983), with weekly growth simply being the monthly growth increment g partitioned into weekly intervals; and c is the allometric length exponent that shapes the function ($c = 1.0$ implies a mortality rate that is inversely proportional to length).

The instantaneous mortality rate from seal predation, $M_{t,y}^{Seal}$, was calculated with a Baranov-type function (Branch 2009) that related the "catch" from seal predation to other sources of natural mortality and the current abundance:

$$M_{t,y}^{Seal} = \left(\frac{E_{t,y}}{N_{t,y}}\right) \frac{\left(M_{t,y}^{Other} + \frac{E_{t,y}}{N_{t,y}}\right)}{1 - \exp\left[-\left(M_{t,y}^{Other} + \frac{E_{t,y}}{N_{t,y}}\right)\right]}. \tag{5}$$

Here, $E_{t,y}$ is the number of individual salmon that were eaten by seals, which is calculated by dividing the weekly total biomass of salmon eaten by the seal population by the average weight (w_t, kg) of the prey:

$$E_{t,y} = \frac{p_t V_y}{w_t}, \tag{6}$$

where p_t is the mean proportion of salmon in the seal diet (in biomass, kg) during week t; and V_y is the weekly biomass of all prey consumed by the seal population. Note that Equation 5 is overly complex for weekly calculations over which the change in N is relatively small; the same basic result can be obtained simply by setting the weekly M_t^{Seal} equal to E_t / N_t. The length-to-weight conversion for prey is an exponential relationship commonly used for salmonids (Froese 2006; Appendix Figure A.1):

$$w_t = \frac{\alpha\left(l_t\right)^{\beta}}{1 \times 10^5}, \tag{7}$$

where l_t is the mean length in week t; and α and β are allometric parameters for juvenile salmonids (Table 3), which were estimated using length and weight data from a previous study (Nelson et al. 2019a). The weekly total biomass of prey consumed by the seal population is estimated as seal population abundance (S_y) times the average daily prey requirement by mass (Q) in kilograms:

$$V_y = \left(S_y Q\right) \times 7. \tag{8}$$

TABLE 3 Symbols, descriptions, values, and sources/references for parameters, variables, and indices included in the harbor seal predation model. CV, coefficient of variation; SD, standard deviation.

Symbol	Description	Value(s)	Source(s)
S_y	Seal abundance	Appendix; Normal (S_y, CV = 0.07)	Olesiuk 2010; Nelson et al. 2019b
Q	Seal daily energetic requirement (kg)	Uniform (1.9, 2.1)	Olesiuk 1993; Howard et al. 2013
p_t	Monthly seal diet proportion	Table 3	Thomas et al. 2017, 2022; Voelker et al. 2020
α	Allometric constant	9.61	Nelson et al. 2019a
β	Allometric constant	3.07	Nelson et al. 2019a
γ	Freshwater/downstream survival proportion	0.70	Bradford 1995; Melnychuk 2009
M^{Ref}	Instantaneous mortality at reference length	Estimated	–
c	Allometric mortality exponent	Estimated	Lorenzen 1996, 2000
g	Monthly growth increment (cm)	3.0	Argue et al. 1983
l_0	Initial prey length (cm)	10.0	Argue et al. 1983; Beamish et al. 2008
l^{Ref}	Reference length (cm)	75	FishBase (www.fishbase.org)
N_{0y}	Initial prey abundance	Table A.3	Korman and Tompkins 2014
σ_y	SD of trawl surveys	CV = 0.30	Beamish et al. 2010
t	Week	$t = 1, ..., T; T = 52$	–
y	Year	2004–2016	–

We assumed that the average harbor seal in the Strait of Georgia requires 1.9–2.0 kg of prey per day (Table 3), which is based on the mean estimated daily requirements from the two most comprehensive bioenergetics studies of harbor seals in the Salish Sea (Olesiuk 1993; Howard et al. 2013). These and other studies suggest that harbor seals consume a diverse diet typical of a generalist predator, but proportions of their major dietary components, such as clupeids (Pacific Herring *Clupea pallasii*), gadoids (Pacific Hake *Merluccius productus* and Walleye Pollock *Gadus chalcogrammus*), and adult salmon, appear to be relatively consistent in the Salish Sea (Lance et al. 2012; Howard et al. 2013; Thomas et al. 2022). Thus, while the average wet weight of prey required to sustain an animal likely varies as a function of its individual diet composition (Rosen and Trites 2000), the agreement between the two studies referenced above—which used diet data from different regions (Strait of Georgia versus Puget Sound) and decades (1980s versus 2000s)—suggests that variability is probably low when generalizing the daily prey requirements over the entire harbor seal population.

Predation model validation

Although the predation model described above provides a mechanistic basis for quantifying the impacts of seal predation relative to other sources of mortality, the estimation of the non-seal mortality component, which is a function of some base mortality rate M^{Ref}, implies additive predation effects from seals—an assumption that is not always true for juvenile salmon populations (Haeseker et al. 2020). Thus, simply adding an estimated base mortality rate to the estimate of seal-related mortality to fit the model to observed data may result in overestimates of actual additive effects (Walters and Christensen 2019). Therefore, we applied the set of equations below as an alternative method to estimate M^{Summer}, the period of high seal predation and a component of total mortality during the first year at sea (M^{Total}). With these equations, we used a basic Monte Carlo simulation to generate a broad "prior" estimate of seal predation that did not depend on estimating a base mortality rate like the one in the predation model. This can be used to validate the previous method without assuming complete additivity of the mortality components. The approach also allowed us to depict uncertainty in parameters for which there was a lack of data and/or precision (e.g., freshwater survival; Table A.1).

First, we note that the total mortality in the first year, M^{Total}, can be partitioned into three broad seasonal components (stanzas):

$$M^{Total} = M^{Fresh} + M^{Summer} + M^{Winter}, \tag{9}$$

where M^{Fresh} is the mortality rate for the short period of downstream migration from hatchery or natural rearing sites to the estuaries where seal consumption begins; M^{Summer} is the mortality rate during the summer months (e.g., May–September) when seal predation occurs; and M^{Winter} is the mortality rate occurring from the fall until the end of the first ocean year of life during the following calendar year. We can partition M^{Summer} into two components:

$$M^{Summer} = M^{Seal} + M^{Other}, \tag{10}$$

where M^{Seal} is the seal predation component; and M^{Other} is a simultaneous, ongoing, and potentially high summer mortality rate due to factors other than seal predation. Recent correlative analyses suggest that such factors may include oceanographic conditions and density-dependent effects from conspecifics (e.g., competition; Sobocinski et al. 2021). However, covariates associated with seal predation were found to be most consistently associated with the best performing models. By varying the M^{Seal} and M^{Other} components of Equation 10, we generated alternative hypotheses about the additive importance of M^{Seal} while maintaining a total M^{Summer} estimate that was consistent with the juvenile trawl survey data.

Scattered observations of freshwater/downstream mortality rates for Coho Salmon from release to ocean entry indicate a substantial loss, with M^{Fresh} as high as 0.69 (Bradford 1995; Melnychuk 2009). The overwinter mortality rate M^{Winter} is likely much lower, probably not exceeding 0.60 (Argue et al. 1983). After the first year of life, the estimates of total instantaneous mortality are probably between 3.0 and 4.0 year^{-1}, on average (Zimmerman et al. 2015).

Note that for any assumed values of M^{Fresh} and M^{Winter}, the M^{Summer} is given in terms of the observed M^{Total} as

$$M^{Summer} = M^{Total} - M^{Fresh} - M^{Winter}. \tag{11}$$

For the summer period, when M^{Seal} and M^{Other} are occurring simultaneously, we used a Baranov-type catch equation similar to the one in the previous section (Equation 4) to predict the net number of fish killed (E') by each of the mortality agents. In particular, the Baranov prediction of seal consumption E' is given by

$$E' = \left(\frac{M^{Seal}}{M^{Summer}}\right) N e^{\left(-M^{Fresh}\right)} \left[1 - e^{\left(-M^{Summer}\right)}\right], \tag{12}$$

where N is the number of smolts at the start of the stanza. This equation simply partitions the total number of summer deaths over that stanza (the number surviving to enter the summer ocean period times the proportion dying in the period, given by $\left[1 - \text{Survival}^{Summer}\right]$). For a given consumption estimate E' and a given set of M^{Fresh} and M^{Winter} values, we can solve the equation for M^{Seal} as

$$M^{Seal} = \frac{E'}{N e^{\left(-M^{Fresh}\right)}} \times \frac{M^{Summer}}{1 - e^{\left(-M^{Summer}\right)}} \tag{13}$$

and then calculate M^{Other} by subtraction ($M^{Other} = M^{Summer} - M^{Seal}$). Note that an indication of nonsensical values in Equation 13 is given by negative estimates of M^{Other}. Varying the E' value in Equation 13 leads to alternative hypotheses about the additivity of mortality caused by the estimated consumption by predators.

The set of equations described above was applied in a Monte Carlo simulation (10,000 draws) using the range of parameter values summarized in Table A.1 to generate a prior distribution for seal-related mortality during the summer, M^{Seal}. Median estimates of annual seal-related mortality rates from the predation model were compared with that prior distribution. If estimates from the predation model are to be considered credible, we would expect them to fall within the range of the prior distribution.

RESULTS

Harbor seal diet

In total, 1484 seal scat samples were collected from all four sites between April and December during the years 2012–2014 (Tables 1–3). The highest monthly sample size occurred in September ($n = 336$), whereas the fewest samples were collected in December ($n = 11$). Samples from Cowichan Bay ($n = 595$) made up the largest percentage (40.1%) of the data set, while the Belle Chain islets produced the fewest ($n = 183$; 12.3%). Juvenile Coho Salmon were present in the harbor seal diet from April through October; juveniles did not occur in the diet during November or December (Table 2). The largest mean monthly diet percentage was 3.8% during July (Table 2). A more detailed analysis of this data set (excluding the 288 samples that were collected from Cowichan Bay in 2014) can be found in Thomas et al. (2017, 2022). Those publications include seal diet proportions of other Pacific salmon species in addition to Coho Salmon, as well as an assessment of the spatial and temporal aspects of the data.

Parameter estimation and model fit

Initial fits of the predation models revealed strong confounding between the parameters M^{Ref} and c. Thus, we elected to fix c and to keep M^{Ref} as a free parameter in the estimation. Previous studies suggested that c is close to 1.0 for Pacific salmonids (Lorenzen 2000); therefore, we chose this value as the “base case” scenario and then evaluated four alternative models, which assumed that c was larger or smaller than 1.0 by 10% or 20%. We compared the alternative models with the base case using Akaike's information criterion corrected for small sample sizes (AIC_c), which suggested no meaningful differences (i.e., differences were <2 AIC_c units; Table A.2). Accordingly, we proceeded to use the predation model with c_s fixed at 1.0. The predation models fit the observed abundance data from trawl surveys reasonably well (Figures 3 and A.2; Table 4). The mean observed September abundance fell within the 95% probability interval of the model-predicted abundance in 13 of the 14 years of data (Figures 3 and A.2). Estimates of M^{Ref} for the predation model was 0.47 year^{-1} (SE = 0.09), which translates to a survival rate at the reference length (l^{Ref}) of 63%.

Predation rates on juvenile Coho Salmon

The median estimated number of juvenile Coho Salmon that were consumed by harbor seals in the first year at sea (May–March) ranged from 6.4 to 7.0 million individuals/year during 2004–2016 (Table 4). This equates to median estimates of proportions of the annual Coho Salmon cohort that were lost to seal predation ranging from 0.46 to 0.59 (Figure 3; Table 4). These estimates suggest that

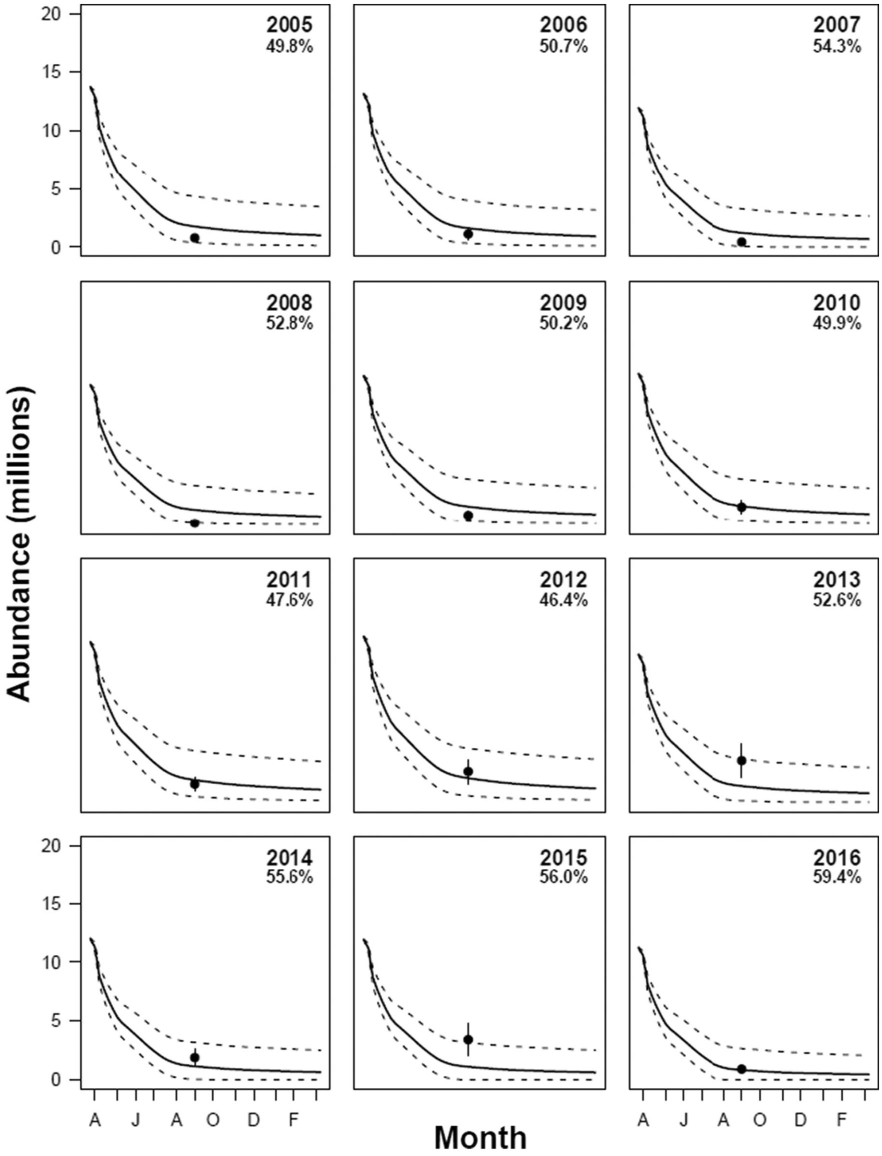

FIGURE 3 Monthly abundance (millions) of juvenile Coho Salmon in the Strait of Georgia from 2004 to 2016. Solid circles depict the observed abundance in September from annual pelagic trawl surveys, with 95% probability intervals shown by vertical black lines. Model-predicted abundance is shown by the decaying black lines, with 95% probability intervals represented by dashed lines. Also shown on each panel is the median percentage of the cohort that was lost to harbor seal predation in the first year.

TABLE 4 Observed and predicted September abundances of juvenile Coho Salmon in the Strait of Georgia. Also shown are the annual estimated proportion of each Coho Salmon cohort that was lost to seal predation in the first year at sea; the total number of individual Coho Salmon eaten in each year; the total instantaneous mortality in the first year from seal predation; and the total natural mortality in the first year, which excludes the freshwater/downstream component. The 95% predictive intervals are shown in parentheses for each quantity.

Year	Observed abundance (millions)	Predicted abundance (millions)	Proportion of juveniles eaten by seals	Total eaten by seals (millions)	Mortality from seal predation	First-year total mortality
2004	0.52 (0.20–0.83)	1.69 (0.40–4.26)	0.51 (0.43–0.58)	7.04 (6.02–8.02)	1.25 (0.80–2.66)	2.64 (1.39–4.60)
2005	0.79 (0.31–1.27)	1.77 (0.37–4.23)	0.50 (0.43–0.57)	6.89 (5.86–7.85)	1.21 (0.78–2.67)	2.59 (1.40–4.64)
2006	1.12 (0.44–1.80)	1.65 (0.30–3.99)	0.51 (0.43–0.58)	6.68 (5.70–7.67)	1.24 (0.81–2.59)	2.64 (1.43–4.91)
2007	0.44 (0.17–0.70)	1.22 (0.11–3.33)	0.54 (0.46–0.63)	6.51 (5.53–7.51)	1.44 (0.91–5.11)	2.83 (1.50–6.76)
2008	0.14 (0.05–0.22)	1.34 (0.15–3.28)	0.53 (0.45–0.60)	6.35 (5.43–7.24)	1.37 (0.85–3.29)	2.75 (1.51–5.88)
2009	0.85 (0.33–1.36)	1.62 (0.30–3.91)	0.50 (0.43–0.58)	6.37 (5.46–7.34)	1.22 (0.80–2.72)	2.61 (1.41–4.80)
2010	1.56 (0.61–2.50)	1.66 (0.38–4.03)	0.50 (0.43–0.57)	6.45 (5.62–7.35)	1.21 (0.78–2.47)	2.61 (1.39–4.55)
2011	1.58 (0.62–2.54)	1.95 (0.47–4.44)	0.47 (0.41–0.55)	6.47 (5.55–7.52)	1.12 (0.75–2.12)	2.49 (1.35–4.30)
2012	2.65 (1.04–4.25)	2.09 (0.64–4.77)	0.46 (0.40–0.54)	6.54 (5.59–7.57)	1.06 (0.71–1.95)	2.45 (1.29–4.01)
2013	3.37 (1.40–5.75)	1.43 (0.18–3.48)	0.52 (0.45–0.61)	6.61 (5.68–7.64)	1.36 (0.82–3.30)	2.72 (1.52–5.58)
2014	1.88 (0.74–3.03)	1.14 (0.02–3.27)	0.56 (0.48–0.64)	6.69 (5.73–7.65)	1.52 (0.92–6.27)	2.93 (1.53–8.94)
2015	3.41 (1.34–5.48)	1.14 (0.02–3.14)	0.56 (0.48–0.64)	6.66 (5.71–7.63)	1.54 (0.96–7.56)	2.91 (1.56–9.09)
2016	0.90 (0.35–1.45)	0.83 (0.02–2.70)	0.59 (0.51–0.69)	6.68 (5.76–7.71)	1.78 (1.05–8.00)	3.21 (1.67–7.21)

during the marine phase, seal predation accounts for between 44% and 59% of natural mortality during the first year. If we assume that freshwater productivity did not change significantly between 1970 and 2016, total annual instantaneous mortality from harbor seal predation on Coho Salmon during the first year at sea increased from 0.10 year^{-1} (95% confidence interval [CI] = 0.08–0.13 year^{-1}) to 1.78 year^{-1} (95% CI = 1.05–8.00 year^{-1}; Figure 4; Table 4). In 1970, seals consumed an estimated 6.7% (95% CI = 5.8–7.7%) of Coho Salmon (Figure 4). Our model estimated that by 2016, the percentage had risen to 59.4% (95% CI = 50.7–68.5%; Figure 5). Median peak mortality from seal predation occurred from ocean entry in late April until early May (Figure 5). A secondary peak in seal-related mortality also occurred in all years during the summer months between July and August.

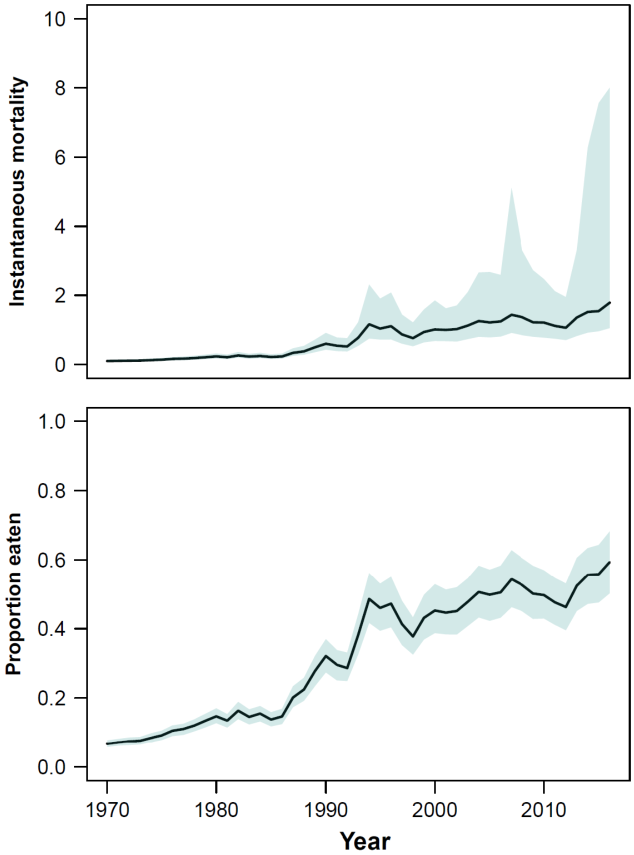

FIGURE 4 Estimated annual total instantaneous mortality from harbor seal predation during the first year at sea for Coho Salmon (top panel) and the proportion of the juvenile cohort that was lost to seal predation (bottom panel) annually in the Strait of Georgia from 1970 to 2016. Solid black lines show the maximum likelihood estimates, while the colored bands depict the 95% probability intervals. Note that these projections assume that the production of natural-origin Coho Salmon stocks in the Strait of Georgia has remained stationary over time, while hatchery releases have decreased in recent years (see Figure 2).

Predation model validation

All annual median estimates of M^{Seal} from the predation model fell between the 2.5% and 97.5% quantiles of the prior distribution (Figure 6). Using the values of E', M^{Fresh}, and M^{Winter} from Equation 12 gives a median M^{Seal} estimate of 1.19 (95% CI = 0.73–1.83). The non-seal mortality rate ($M^{Fresh} + M^{Other} + M^{Winter}$) for Coho Salmon was 2.28 (95% CI = 1.67–2.92), which was comparable to the observed survival and mortality rates observed in the late 1970s, when survival rates for Coho Salmon during their first year at sea typically ranged between 10% and 15% (Zimmerman et al. 2015). The M^{Seal} estimates were of course sensitive to the estimates of seal consumption E' and were also very sensitive to assumed (initial) smolt numbers N_0. The estimated natural smolt abundances were likely biased upward due to incomplete sampling of coded wire tags (CWTs) in the escapement (Korman and Tompkins 2014). Assuming a lower N due to the CWT bias problem results in higher estimates of M^{Seal}. Likewise, higher assumed values for M^{Fresh} lead to higher M^{Seal} estimates, and higher estimates of M^{Winter} lead to lower estimates of M^{Seal}.

DISCUSSION

We combined harbor seal diet data from 1484 fecal samples with a quantitative modeling framework to estimate the impacts of harbor seal predation on juvenile Coho Salmon in the Strait of Georgia, British Columbia. Our analysis suggests that for the past few decades, predation by harbor seals during spring and summer has been a significant source of natural mortality for Coho Salmon in the first year of their marine stage, despite this species being a minor component of the harbor seal diet. Our models estimate that harbor seals consumed an annual average of 46–59% of juvenile Coho Salmon (6–7 million fish) from 2004 to 2016. These consumption estimates, when combined with abundance data for seals and salmon, suggest that mortality rates from seal predation have increased significantly since the 1970s. These trends provide evidence for a causal relationship between seal abundance—which has been stabilized or near carrying capacity for the past two decades—and the chronically low marine survival of juvenile Coho Salmon.

Our study complements previous work investigating the impacts of harbor seal predation on Coho Salmon in the Salish Sea (Thomas et al. 2017; Nelson et al. 2021) and is the first to quantify possible impacts of pinniped predation on juvenile Coho Salmon in the Strait of Georgia at an ecosystem scale. The predation and mortality estimates presented here are potentially useful for quantifying

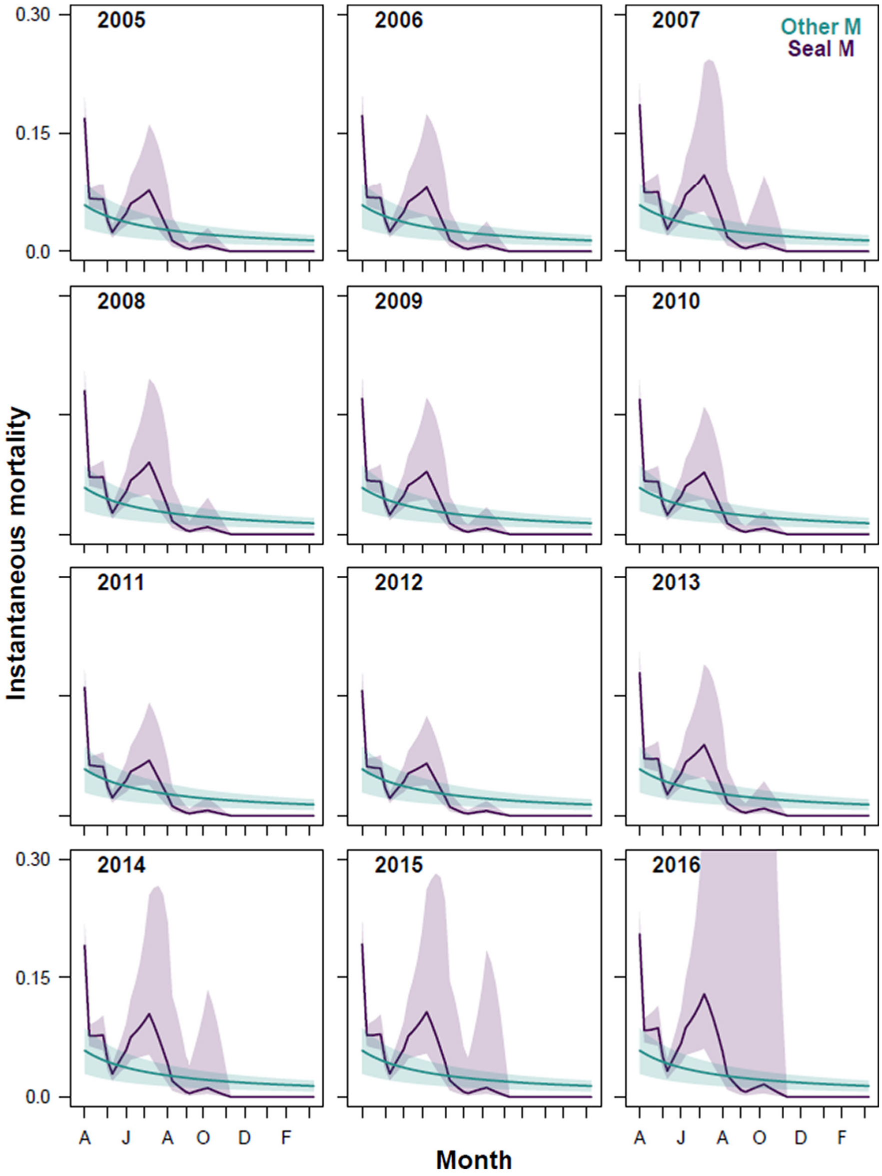

FIGURE 5 Weekly instantaneous mortality rate (*M*) of Coho Salmon from harbor seal predation (purple) and from other sources (teal) during the first year at sea. Solid lines show the median estimate, and shaded bands depict the 95% probability intervals.

predator–prey dynamics within the context of an ecosystem-based fisheries management framework (Marshall et al. 2018) and ecosystem modeling, in addition to updating the current understanding of factors influencing marine survival for Pacific salmon stocks of high conservation concern.

Predation impacts to juvenile Coho Salmon

As shown in previous studies, juvenile Coho Salmon comprise a relatively small fraction of the annual harbor seal diet in the Strait of Georgia and the Salish Sea (Lance et al. 2012; Thomas et al. 2017; Nelson et al. 2021). However, the prey consumption calculations presented here and in other studies show that even small diet proportions (<5%) of juvenile salmon can equate to large numbers of individual prey being consumed (Chasco et al. 2017a, 2017b; Nelson et al. 2021). Even though juvenile Coho Salmon never exceeded 5% of the overall diet in any given month, we estimated that harbor seals consumed an average of 46–59% of the juvenile Coho Salmon entering the ocean during the spring in the first year at sea. This is somewhat higher than previous estimates of seal predation on Coho Salmon in Puget Sound (Nelson et al. 2021), which may reflect the significantly higher densities of predators in the Strait of Georgia (Nelson et al. 2019b). Our analysis estimated an increase in total instantaneous mortality of 2.0 year^{-1} for juvenile Coho Salmon, which suggests that the increase in

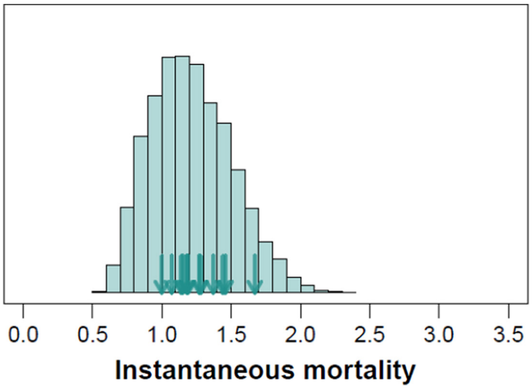

FIGURE 6 Prior distribution for harbor seal-related instantaneous mortality rates for Strait of Georgia Coho Salmon during their first year at sea. The histogram (solid bars) is based on 10,000 parameter combinations drawn from the uniform distributions shown in Table A.1. Individual arrows along the *x*-axis show annual median estimates from the predation model for 2004–2016.

the magnitude of seal predation between the 1970s and the present day could explain most of the increase in total marine mortality throughout the same time period (Table A.4).

Most recent research efforts related to pinniped predation on salmon in the northeast Pacific and Salish Sea ecosystems have focused on impacts to Chinook Salmon *O. tshawytscha*, whereas ours is the first study to quantify consumption and mortality rates of juvenile Coho Salmon in the Strait of Georgia basin. Coho Salmon currently do not have the same levels of federal, state, and provincial protections that Chinook Salmon have in the Salish Sea, but it is important to acknowledge their benefit to ecosystem function as potential prey for southern resident killer whales (Ford et al. 2016), in addition to their contribution to Indigenous, commercial, and recreational fisheries in the region (Bendriem et al. 2019). Rapid declines in Coho Salmon abundance since the 1980s have been a major driver of the increasingly restrictive fisheries policies in the Strait of Georgia and outside waters (Walters et al. 2019).

Our work suggests that harbor seal predation is a significant factor affecting the early marine survival of Coho Salmon in the Strait of Georgia, as our model predicts that one out of every two young Coho Salmon is eaten by seals within the first 7 months in marine waters. The marked decline in Coho Salmon marine survival between the early 1970s and late 1990s appears to show a very strong association with the mortality rates predicted in this study. Recent work by other researchers has also established a negative statistical correlation between seal density and Coho Salmon marine survival rates in the Salish Sea, even while controlling for several other abiotic and biotic covariates (Sobocinski et al. 2021). Although seal abundances remained nearly constant between 2004 and 2016 (Figure 2), our model predicted that year-to-year mortality rates may be explained by hatchery release numbers, which decreased significantly over this time period. With a stable seal population, this would imply an increase in per-capita mortality rates. It is unclear whether this is simply driven by the model formulation or whether predation rates may be increasing from less "buffering," which can occur at higher prey abundances (e.g., Malick et al. 2022).

Management implications

The seasonal dynamics of seal-related mortality on juvenile Coho Salmon may have important implications for designing effective management strategies that might actively try to control predator populations. Our models predict that mortality from seal predation spikes during the middle of the summer for juvenile Coho Salmon after large numbers of young fish have departed estuarine and nearshore habitats to rear in the offshore pelagic environment. Relative predation rates appear to be higher upon ocean entry for Coho Salmon compared to Chinook Salmon, as observed in a recent study during which tagged harbor seals along east Vancouver Island responded to pulses of hatchery-released juvenile Coho Salmon while ignoring much larger releases of Chinook Salmon from the same hatchery (Allegue et al. 2020). Similarly, another recent study conducted in Puget Sound, Washington, found that early marine mortality rates for Coho Salmon and steelhead were considerably higher than those for more abundant Chinook Salmon (Malick et al. 2022); those authors speculated that this could be due to an abundant predator's preference for larger-bodied juvenile salmon. Previous modeling studies (Chasco et al. 2017b), including unpublished work associated with this analysis (Nelson 2020), also suggest that predation rates on juvenile Coho Salmon in the Strait of Georgia could be markedly higher than those for juvenile Chinook Salmon.

Research on foraging patterns, growth, and survival of juvenile Coho Salmon suggests that individuals surviving to mid- and late summer are typically larger and have a higher probability of survival (Duffy and Beauchamp 2011; Gamble et al. 2018). Thus, predation on these individuals is likely to have a much higher relative impact on the cohort compared to individuals that succumb to mortality shortly after ocean entry in late spring. With these seasonal mortality dynamics in mind, it appears that management alternatives involving only targeted culls of individual predators within river mouths or estuaries are unlikely to have substantial benefits due to the delayed compensatory mortality that occurs later in the summer. Such policies would be "lose–lose" options, which would likely incur the condemnation of some stakeholders while not producing measurable benefits for others. It is unclear whether the high seal predation rates on Coho Salmon during the summer months reflect predators targeting young salmon or are due to temporal and spatial overlap with species like Pacific Herring and Pacific Hake, which are the preferred prey of harbor seals in the Salish Sea ecosystem (Trites and Rosen 2019; Trzcinski 2020).

Model assumptions and limitations

Despite accounting for uncertainty in several key model inputs and parameters in predation models and confronting those models with an alternative set of equations and predictions, this analysis does have several limitations. First, the empirical foundation of this study is the estimates of the monthly proportions of juvenile Coho Salmon in the harbor seal diet. Accurately quantifying and describing predator diets by using DNA and hard structures (extracted from fecal material) are notoriously difficult for ecologists (Bowen and Iverson 2013). Also, developing a sampling protocol that can reliably differentiate across temporal and spatial strata adds a formidable layer of uncertainty (Trites and Joy 2005).

Although the methods we used represent an improvement from studies performed almost three decades earlier (Olesiuk et al. 1990), the sampling design used to produce our data set potentially introduces bias with regard to representation of the harbor seal diet in the Strait of Georgia. Of the four sampling sites that were used in our study (Figure 1), two of them (Fraser River and Cowichan Bay) are unambiguously estuarine habitats. The seal haulout near Comox likely represents a hybrid of estuary- and nearshore-type habitat in the Strait of Georgia, and the Belle Chain islets are rocky reef areas. Thus, it is reasonable to assume that our samples could be biased toward animals in estuary sites, which may have higher encounter rates with juvenile salmon because of their proximity to river mouths. However, it is important to acknowledge that some harbor seals using estuary haul-outs almost certainly spend time foraging in non-estuary areas (Peterson et al. 2012; Thomas et al. 2017). Additionally, a closer examination of the prey proportions by site revealed that non-estuary samples had among the highest proportions of juvenile Chinook Salmon of any stratum (Thomas et al. 2017, 2022). This finding was also consistent with a previous study that documented seal diets in the San Juan Island archipelago in Washington State, which is located less than 50 km from the Belle Chain islets (Lance et al. 2012). This evidence suggests that the data we used are likely representative of the Strait of Georgia harbor seal diet.

The model-predicted mortality rates shown here require an estimate of the number of young salmon that are at risk of seal predation each year: (1) the sum of hatchery-origin smolts, which is known from detailed release records; and (2) what we assume is a constant *average* number of naturally produced salmon originating from tributaries in the Strait of Georgia. Our model projections were quite sensitive to this input and, by extension, the freshwater downstream survival that scaled the estimate. Because abundance (i.e., number of fish at risk of predation) is inversely related to seal mortality rates, conservative estimates of freshwater survival rates will likewise predict relatively conservative impacts of predation. Survival no doubt varies considerably by stock and location, but our estimates of 70% freshwater survival for Coho Salmon are probably conservative. Coho Salmon survival rates during freshwater migration are likely much lower than the 70% estimate used here (Bradford 1995; Melnychuk 2009); use of lower survival rate estimates would also increase our predation estimates.

Finally, the predation estimates generated here and in similar studies (Chasco et al. 2017a, 2017b) are sensitive to assumptions about prey size, particularly during the period shortly after ocean entry, when smolts are relatively small (<12 cm) and growing in mass at exponential rates. Our model assumes that harbor seals in the Strait of Georgia consume juvenile Coho Salmon at an average size equal to those sampled in scientific surveys. In light of previous work suggesting that harbor seals may select for larger individual prey relative to available prey (Tollit et al. 1997; Nelson et al. 2019a; Allegue et al. 2020; Malick et al. 2022), it is possible that our assumed prey size is biased low (Nelson et al. 2021). Correcting for this bias would reduce the estimated number of individual salmon that were eaten annually. However, the observed prey sizes from a sample of Coho Salmon otoliths recovered from scat samples (see Thomas et al. 2017: their fig. 6) confirm that prey size over time is comparable with our assumed pattern of Coho Salmon growth (Figure A.1).

Future research on the impacts of seal predation on Coho Salmon would benefit from a modeling framework that is spatially explicit and accounts for movement of predators and prey throughout the entire Salish Sea ecosystem. Some estimates have suggested that a large fraction of Coho Salmon rearing in the Strait of Georgia may be of Puget Sound origin (Beacham et al. 2016). Similarly, the proximity of the Fraser River delta to north Puget Sound, in addition to the high abundance of natural- and hatchery-origin Coho Salmon emigrating from the Fraser River, suggests that a significant number of Canadian Coho Salmon stocks likely rear in U.S. waters for a substantial period of time. Studies on the movements of individual harbor seals in the Salish Sea ecosystem revealed home ranges suggesting that the migration of animals across boundaries is common (Peterson et al. 2012), which could also influence efforts to quantify the impacts of predation.

It is also important to acknowledge that other predators, including fish (Beamish et al. 1992), birds, and mammals (Nelson et al. 2019a, 2019b; Sherker et al. 2021), may have meaningful impacts on juvenile Coho Salmon. With advances in environmental DNA processing technology, predator scat samples from other salmon predators could be easily added to our modeling framework, thus facilitating a comparison of the relative importance of predation sources.

Ecosystem considerations

Although multiple model inputs and assumptions contribute to uncertainty in the analysis presented here, our findings provide evidence that harbor seal predation could be an important driver of marine survival during the first year at sea for Coho Salmon in the Strait of Georgia. The recent correlative findings (Sobocinski et al. 2021), in addition to diet analyses (Lance et al. 2012; Thomas et al. 2017), suggest that the control of predator populations might facilitate the recovery of Coho Salmon stocks. Although predator removals would provide a direct means to test the existence of a causal relationship between predation and declining salmon stocks, as opposed to continuing to devote resources to further data gathering and modeling exercises, it is important to acknowledge that non-additive mortality from other sources may complicate such management alternatives.

A recent study on out-migrating steelhead in the Columbia River basin found evidence that the removal of avian predators like double-crested cormorants *Phalacrocorax auritus* and Caspian terns *Hydroprogne caspia* would not meaningfully increase overall survival, as fish navigated a gauntlet of potential predators in a heavily altered riverine environment (Haeseker et al. 2020). The Strait of Georgia and the greater Salish Sea ecosystem have also undergone major changes, with potential threats to fish populations from climate change, pathogens, and contaminants, all of which have the potential to mediate predator–prey interactions (Tucker et al. 2016; Selden et al. 2018; Mordecai et al. 2019). It is also important to recognize that the removal of predators to benefit one species could affect other species within the ecosystem (Lessard et al. 2005), such as transient killer whales that have become increasingly dependent over the past three decades on consuming harbor seals in the Salish Sea (Shields et al. 2018). Thus, while studies such as ours are imperative for understanding the ecology of Pacific salmon and for developing realistic strategies for their recovery, we caution others to temper drawing simple conclusions about the potential efficacy of removing predators with the recognition that the surrounding marine ecosystem is inherently complex.

Recent policy discussions about reducing harbor seal populations in the Strait of Georgia have focused mainly on the quantitative uncertainty related to the numbers of young salmon consumed (Trites and Rosen 2019; Trzcinski 2020). However, the most important uncertainty about such policies actually concerns whether seal predation is causing additive mortality in the first place (Walters and Christensen 2019) or whether mortality inflicted by seals is concentrated on juveniles that would have died anyway due to other factors, such as disease, high water temperatures, and lack of prey. There is no way, in principle, to resolve this deeper uncertainty by continued predator diet studies and more precise modeling results; rather, a reduction in seal abundance would be necessary to see whether mortality rates decrease as predicted. Essentially, any active population control of the harbor seal population in the Strait of Georgia should be viewed as an adaptive management experiment over one to two decades, with a highly uncertain outcome.

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CONFLICT OF INTEREST STATEMENT

The authors do not declare any conflicts of interest involved in the production of this manuscript.

DATA AVAILABILITY STATEMENT

Harbor seal diet data used in this study are available in Thomas et al. (2022): https://www.nature.com/articles/s41597-022-01152-5.

ETHICS STATEMENT

The harbor seal scat samples were collected under Fisheries and Oceans Canada Marine Mammal Research Licenses (MML 2011-10 and MML 2014-07) and a University of British Columbia Animal Care Permit (A11-0072).

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APPENDIX

Additional Tabular Data and Figures

TABLE A.1 Ranges of parameter values used to formulate the prior distributions for harbor seal-related instantaneous mortality of Coho Salmon in the Strait of Georgia.

Parameter	Description	Minimum	Maximum
$N^{Natural}$	Initial abundance of natural-origin smolts (millions)	8.00	15.00
E'	Number of prey consumed by harbor seals (millions)	4.00	8.00
M^{Fresh}	Freshwater/downstream mortality	0.22	0.69
M^{Winter}	Overwinter mortality	0.20	0.50
M^{Total}	Total mortality (first year)	3.00	4.00

TABLE A.2 Values of Akaike's information criterion corrected for small sample sizes (AIC_c) for predation models across multiple values of the allometric length exponent *c*.

	c				
Model	**0.80**	**0.90**	**1.00**	**1.10**	**1.20**
AIC_c	−1.49	−1.49	−1.49	−1.38	−1.39

TABLE A.3 Mean annual harbor seal abundance in the Strait of Georgia and annual total hatchery releases of Coho Salmon from Strait of Georgia tributaries. Also shown is the estimated wild production from Strait of Georgia tributaries. Seal abundances were estimated using a state-space model fitted to aerial survey data (Nelson et al. 2019b). Annual hatchery releases were collated using data from the Regional Mark Information System database (www.rmpc.org; accessed June 2019).

Year	Seals	Hatchery releases (millions)	Wild production (millions)	Total
2004	41,696	9.3	7.4	16.7
2005	40,625	9.1	7.4	16.5
2006	39,582	8.2	7.4	15.6
2007	38,565	6.5	7.4	13.9
2008	37,552	6.6	7.4	14.0
2009	37,915	7.6	7.4	15.0
2010	38,258	7.9	7.4	15.3
2011	38,605	9.0	7.4	16.4
2012	38,955	9.6	7.4	17.0
2013	39,308	7.4	7.4	14.8
2014	39,631	6.6	7.4	14.0
2015	39,631	6.5	7.4	13.9
2016	39,631	5.5	7.4	13.9

TABLE A.4 Estimated annual harbor seal-related instantaneous mortality rates and proportion of juvenile Coho Salmon eaten during the first year at sea from 1970 to 2016. Estimates are extended from Tables 3 and 4. Shown are the median estimates for each year, with 95% predictive intervals given in parentheses.

Year	Mortality from seal predation	Proportion of juveniles eaten by seals
1970	0.10 (0.08–0.13)	0.07 (0.06–0.08)
1971	0.11 (0.08–0.14)	0.07 (0.06–0.08)
1972	0.11 (0.08–0.15)	0.07 (0.06–0.09)
1973	0.11 (0.09–0.15)	0.08 (0.07–0.09)
1974	0.13 (0.10–0.17)	0.08 (0.07–0.10)
1975	0.14 (0.10–0.19)	0.09 (0.08–0.11)
1976	0.16 (0.12–0.21)	0.11 (0.09–0.12)
1977	0.17 (0.13–0.23)	0.11 (0.09–0.13)
1978	0.19 (0.14–0.25)	0.12 (0.10–0.14)
1979	0.21 (0.16–0.28)	0.13 (0.12–0.15)
1980	0.23 (0.18–0.32)	0.15 (0.13–0.17)
1981	0.21 (0.16–0.29)	0.13 (0.11–0.15)
1982	0.26 (0.20–0.36)	0.16 (0.14–0.19)
1983	0.23 (0.17–0.31)	0.15 (0.12–0.17)
1984	0.25 (0.19–0.34)	0.16 (0.13–0.18)
1985	0.22 (0.17–0.30)	0.14 (0.12–0.16)
1986	0.23 (0.17–0.32)	0.15 (0.12–0.17)
1987	0.34 (0.25–0.47)	0.20 (0.17–0.23)
1988	0.38 (0.28–0.54)	0.22 (0.19–0.26)
1989	0.50 (0.36–0.72)	0.28 (0.23–0.32)
1990	0.60 (0.43–0.91)	0.32 (0.27–0.37)
1991	0.54 (0.39–0.78)	0.30 (0.25–0.34)
1992	0.52 (0.38–0.76)	0.29 (0.25–0.33)
1993	0.77 (0.54–1.22)	0.38 (0.33–0.44)
1994	1.16 (0.75–2.31)	0.49 (0.42–0.56)
1995	1.04 (0.72–1.90)	0.46 (0.39–0.53)
1996	1.11 (0.72–2.08)	0.47 (0.40–0.55)
1997	0.87 (0.60–1.44)	0.41 (0.35–0.48)
1998	0.76 (0.53–1.21)	0.38 (0.33–0.43)
1999	0.94 (0.64–1.59)	0.43 (0.37–0.50)
2000	1.01 (0.68–1.85)	0.45 (0.39–0.53)
2001	1.00 (0.68–1.62)	0.45 (0.38–0.51)
2002	1.02 (0.66–1.70)	0.45 (0.38–0.52)
2003	1.12 (0.73–2.09)	0.48 (0.41–0.55)
2004	1.25 (0.80–2.66)	0.51 (0.43–0.58)
2005	1.21 (0.78–2.67)	0.50 (0.42–0.57)
2006	1.24 (0.81–2.59)	0.51 (0.43–0.58)
2007	1.44 (0.91–5.11)	0.54 (0.46–0.63)
2008	1.37 (0.85–3.29)	0.53 (0.45–0.60)
2009	1.22 (0.80–2.72)	0.50 (0.43–0.58)
2010	1.21 (0.78–2.47)	0.50 (0.43–0.57)
2011	1.12 (0.75–2.12)	0.48 (0.41–0.55)
2012	1.06 (0.71–1.95)	0.46 (0.40–0.53)
2013	1.36 (0.82–3.30)	0.52 (0.45–0.61)
2014	1.52 (0.92–6.27)	0.56 (0.47–0.63)
2015	1.54 (0.96–7.56)	0.56 (0.48–0.64)
2016	1.78 (1.05–8.00)	0.59 (0.50–0.68)

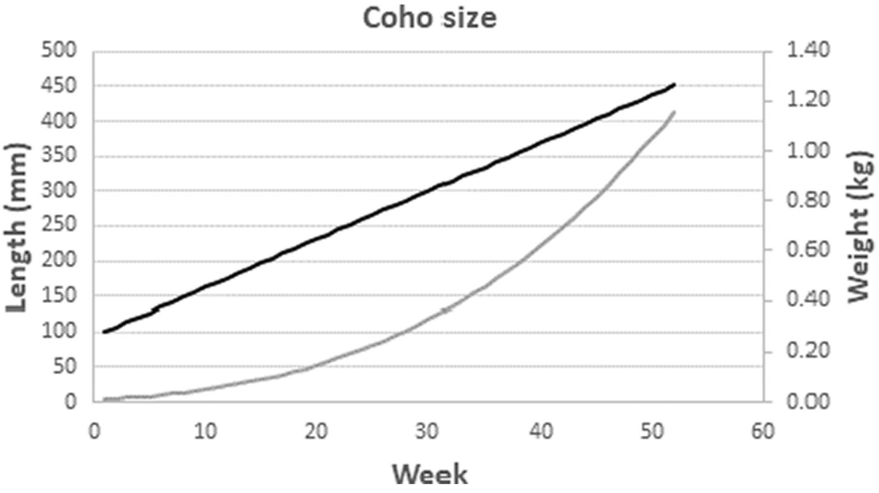

FIGURE A.1 Coho Salmon length (black) and weight (gray) over time for the harbor seal predation model.

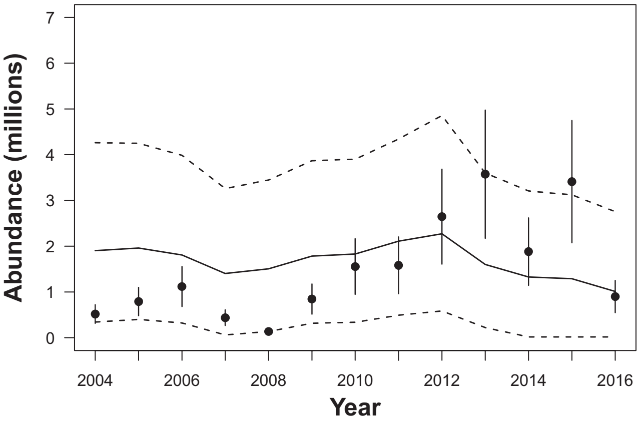

FIGURE A.2 Predicted versus observed September abundances of Coho Salmon between 2004 and 2016. Filled circles depict the observed abundances documented in annual pelagic trawl surveys, with vertical lines representing 95% confidence intervals. The solid black line shows the model-predicted abundance, and dashed lines represent the 95% probability interval associated with the predicted abundance.