PREDATOR-PREY INTERACTIONS BETWEEN HARBOUR SEALS (*PHOCA VITULINA*) AND PACIFIC SALMON (*ONCORHYNCHUS SPP.*) IN THE SALISH SEA

by

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Abstract

Populations of Chinook (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) have experienced significant declines in abundance and productivity over the last 50 years in the Salish Sea as harbour seals (*Phoca vitulina*) recovered from hunting and culling. Some have hypothesized that increased predation by seals may be responsible for the declines in salmon survival, and their failure to recover after reductions in fishing effort. However, it is not known if these correlations exist for every population of salmon in the Salish Sea, or how many young Chinook and coho salmon are consumed by seals each year. I developed mathematical and statistical models to investigate the potential causal relationship between seal predation and declines in Chinook and coho salmon populations in the Salish Sea. I also used simulation modeling to evaluate outcomes that may result if managers reduced British Columbia's harbour seal population to promote the recovery of salmon populations. I found that harbour seal densities were strongly negatively associated with productivity of most wild Chinook salmon populations in the Salish Sea and Washington Coast that were included in the study. Integrating recently collected seal diet data with a novel predation model indicates that large numbers of juvenile Chinook and coho salmon are eaten by seals, and that predation-related mortality has likely increased significantly over the last 50 years. The results of my simulation model suggest both lethal removals and contraception could reduce the seal population, but that important tradeoffs exist between the two approaches. Overall, my findings increase understanding of the role that marine mammal predation plays in the early marine life stage of juvenile salmon, and identifies potential outcomes and tradeoffs of actively managing predator populations.

Lay Summary

Chinook and coho salmon support indigenous, commercial, and recreational fisheries along the west coast of North America, and are important prey for other marine organisms. To understand the role that harbour seal predation has played in recent declines of salmon populations, I developed mathematical models to evaluate whether seal predation is negatively impacting their survival. I also simulated how the harbour seal population in British Columbia may respond to efforts to reduce their population size, which could help salmon populations recover. I found evidence that seal predation may be a significant source of mortality on juvenile salmon in the Salish Sea, and that controlling the seal population with lethal and non-lethal methods may be viable options for managers. My findings increase current understanding of factors that influence survival of juvenile salmon in the Pacific Ocean, and demonstrate how the seal population in British Columbia could be actively managed.

Preface

This dissertation is one component of a larger research effort entitled: "Assessing the impact of marine mammals on the recovery of Pacific salmon and Atlantic cod", which is part of a collaboration initiative funded by the Natural Sciences and Engineering Research Council of Canada (NSERC): the Canadian Fisheries Research Network (CFRN). The objective of the CFRN projects were to investigate research questions relevant to Canadian fisheries through fostering collaboration among members of industry, government, and academia. The Pacific Salmon Foundation (PSF) also provided funding support for the harbour seal diet studies in the Strait of Georgia between 2012-2014, which were led by Dr. Austen Thomas and myself.

Harbour seal diet studies were conducted by researchers from the University of British Columbia under Federal Permits MML 2011-10 and MML 2014-07 from the Department of Fisheries and Oceans, Canada, and under Animal Care Permit A11-0072, which was approved by the University of British Columbia.

Chapter 2: A version of this chapter has been published in a peer-reviewed journal with the following citation: "Nelson, B. W., C. J. Walters, A. W. Trites, and M. K. McAllister. 2019. Wild Chinook salmon productivity is negatively related to seal density and not related to hatchery releases in the Pacific Northwest. Canadian Journal of Fisheries and Aquatic Sciences 76:447-462." This study was conducted, analyzed and written by BWN under the supervision of MKM, AWT and CJW. BWN gathered, vetted, and collated the data; BWN, MKM and CJW developed the modeling framework, and all co-authors contributed to the editing of the manuscript.

Chapter 3: A version of this chapter has been submitted to a peer-reviewed journal and is currently under review with the following citation: "Nelson, B. W., M. K. McAllister, A. C. Thomas, A. W. Trites, and C. J. Walters. Quantifying impacts of harbour seal predation on juvenile Chinook and coho salmon in the Strait of Georgia, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences. *In review*". This study was conducted, analyzed and written by BWN under the supervision of CJW, MKM and AWT. BWN and AWT designed and developed the field sampling protocols. BWN organized the field work and collected the data; BWN and CJW developed the modeling framework, and all co-authors contributed to the editing of the manuscript.

Chapter 4: This study was conducted, analyzed and written by BWN under the supervision of MKM, CJW and AWT. BWN, MKM, and CJW developed the modeling framework, and all co-authors contributed to the editing of the manuscript.

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Chapter 1: General introduction

1.1 Pinniped-fisheries conflicts

Protection from hunting and culling has led to the recovery of many populations of marine mammals throughout the world (Read and Wade 2000; Bowen and Lidgard 2013). Historically, culls or bounties on marine mammals were implemented in response to perceived impacts to commercially valuable fish stocks, competition with fisheries, and damage inflicted to fishing gear (Yodzis 2001; Read 2008; Oliveira et al. 2020). In North America, for example, protection of marine mammals under the Fisheries Act in Canada and the Marine Mammal Protection Act in the United States in the early-1970s led to recovery of several populations of marine mammals, especially pinnipeds (seals and sea lions) (Read and Wade 2000; Jeffries et al. 2003; Brown et al. 2005; DFO 2008; Olesiuk 2010).

Coincident with protection of marine mammal populations in the middle twentieth century was an overall increase in catches (landings) by commercial fisheries worldwide (Worm et al. 2009), and the eventual realization that many fish stocks were over-fished (Pauly et al. 2002; Hilborn et al. 2003; Branch et al. 2011). While some overfished stocks were successfully rebuilt following reductions in fishing mortality (Murawski 2010), others, such as Atlantic cod and some species of Pacific salmon, remained at low abundance despite extremely low levels of fishing (Trzcinski et al. 2006). Along with environmental factors like climate change, increases in predation from marine mammals were posed as a possible explanation for the failure of some fish stocks to recover (Palsson et al. 2009; Chasco et al. 2017a, b; Neuenhoff et al. 2018; Walters et al. 2020).

1.2 Declines of Chinook and coho salmon in the northeastern Pacific Ocean

Like Atlantic cod, harvesting of Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon by modern commercial fisheries in the eastern Pacific peaked in the 1970s and 1980s, and subsequently experienced drastic declines in abundance and productivity (Nehlsen et al. 1991; Beamish et al. 1995; Beamish et al. 1999; Beamish et al. 2010; Beamish et al. 2012a; Preikshot et al. 2013). Populations in southern British Columbia, Washington, Oregon, and California have seen the most precipitous declines. Researchers have proposed a number of plausible biotic and abiotic explanations: loss of freshwater and marine habitat (Nehlsen et al. 1991; Magnusson and Hilborn 2003); overfishing (Rutter 1997); interspecific competition (Ruggerone and Nielsen 2004; Ruggerone and Goetz 2004; Springer and van Vliet 2014); changes in ocean conditions (Beamish et al. 1995; Coronado and Hilborn 1998; Mueter et al. 2005), and changes in abundance of prey like herring and zooplankton (Beamish et al. 1994; Beamish et al. 2000a; Mackas et al. 2001; Beaugrand and Reid 2003; Ruzicka et al. 2011; Mackas et al. 2013).

While it remains unclear what factor, or composite of factors, is driving productivity of Chinook and coho salmon populations in the eastern Pacific, research suggests that survival rates within the first several months of the marine life stages are the most important for determining (pre-fishery) abundance (Beamish et al. 2010a, b; Neville et al. 2015). Total marine survival (from natural mortality) for coho salmon in the Strait of Georgia decreased from around 10% in the 1980s to under 2% by the 1990s and has remained stable (Beamish et al. 2000b). Chinook salmon marine survival rates (from natural mortality) dropped from around 5% to less than 1% over the same time period (PSC 2014; Ruff et al. 2017; Kendall et al. 2020). Scientists and managers identified the decreasing trends in Chinook and coho salmon populations, and implemented measures to reduce commercial harvest rates significantly during the 1990s, particularly for coho in the Salish Sea region (PSC 2013, 2014b). Harvest rates on coho salmon that averaged between 65-80% in the 1970s and 1980s dropped to well under 10% in the Strait of Georgia, British Columbia. This included recreational harvest of both species, a boon to urban and rural economies in British Columbia and Washington State. Despite the reduction in fishing mortality from the 1990s to present day, marine survival rates remain low, recruitment remains depressed, and some populations have been classified as "threatened" by the Endangered Species Act (United States), and designated as threatened and endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (NMFS 1997; Walters et al. 2019).

1.3 Harbour seals in the Salish Sea

The failure of Chinook and coho salmon populations to respond to reduced fishing mortality has led to speculation that changes in natural mortality from upper-trophic levels of the ecosystem may be impeding recovery of some salmon populations (Miller et al. 2013). While avian predation on out-migrating smolts has been the topic of some recent research (Evans et al. 2012; Sebring et al. 2013; Sherker 2020), pinnipeds are often assumed to inflict the most damage on salmon populations, likely because of their size and their tendency to interact with prey at the surface where they are visible to fishermen, scientists and the general public. Further, in regions like the Salish Sea, populations of seals and sea lions are at historically high abundances. Olesiuk (2010) estimated that the Strait of Georgia is home to around 40,000 harbour seals (*Phoca vitulina*) as recently as 2008, up from fewer than 5,000 in 1970. Rates of increase were similar to the south in Puget Sound, where the harbour seal population saw a 7 to 10-fold increase in abundance from 1970-2000 (Jeffries et al. 2003). Both populations have been stable for the past 20 years. Populations of Steller sea lions (*Eumetopias jubatus*) in British Columbia, a species declining in Russia and western Alaska, have increased at a near-exponential trajectory since the 1970s (DFO 2008). California sea lions (*Zalophus californianus*) have also shown marked increases in abundance throughout their range in the eastern Pacific (NMFS 1997). Unsurprisingly, these recoveries that coincided with decreased abundances of commercially important species like salmon and rockfish have generated increased interest in the foraging ecology of pinnipeds.

1.4 Harbour seal foraging ecology

Much of the research on diet and foraging ecology of pinnipeds in the northeastern Pacific focuses on harbour seals in the Salish Sea (Strait of Georgia, Puget Sound, and Strait of Juan de Fuca), and the California current ecosystem on the west coast of the United States. A combination of field (e.g., visual surveys) and laboratory techniques are usually combined to describe the diets of harbour seals, or to estimate impacts to fish species of interest (Brown and Mate 1983; Bigg et al. 1990; London 2006; Wright et al. 2007; Lance et al. 2012). Studies that attempt to quantify impacts by visual observation of seal-salmon interactions are prone to imprecise estimates due low coverage of spatial and temporal strata, and from uncertainty associated with identification of prey species. For example, Wright (2007) estimated that 500-750 harbour seals consumed 503-1,818 coho salmon returning to an estuary in Oregon, based on approximately 760 hours of visual observations. Visual survey protocols are also unable to estimate juvenile consumption, as predation usually occurs beneath the surface for small prey items.

The role that harbour seals may have played in the declines of Pacific salmon since the 1970s, or the extent to which predation may be preventing their recovery, is still uncertain. However, it is clear from diet studies that salmon are an important source of prey for seal populations in British Columbia and the northwestern United States (Olesiuk 1993; Lance et al. 2012; Howard et al. 2013; Adams et al. 2016; Thomas et al. 2017). Further, it is evident that, under certain conditions, seals are capable of consuming significant percentages of salmon runs during the migration of adults to the spawning grounds. In the Puntledge River in British Columbia, Bigg (1990) estimated that harbour seals ate 46% of the fall run of Chinook salmon in 1989. Wright (2007) estimated 20% of returning coho were lost to seal predation in the Alsea River on Oregon’s coast in 2002. A study by Thomas et al. (2017) estimated that, between April and July, coho and Chinook salmon comprise up to 7% and 15% of total harbour seal diet in nearshore areas in the Strait of Georgia, respectively. Considering the small size (5-15 grams) of young salmon during the first few months in the marine environment, this suggests consumption of juveniles during the spring may be substantial.

Attempts to quantify predation on salmon are also made using bioenergetics modeling approaches that use data from fecal material (scats) to describe diet composition (e.g., Olesiuk 1993; Howard et al. 2013). Most of these studies do not attempt to quantify impacts to juveniles and typically present consumption estimates as total mass consumed annually or seasonally. This information is of limited use to natural resource managers, who presumably require estimates of total *individuals* consumed to make meaningful inferences via quantitative fisheries stock assessment or population dynamics modeling (Walters 1986; Hilborn and Walters 1992). The number of young salmon eaten by harbour seals has been estimated (Chasco et al. 2017a, b), but certain assumptions used in these models are inconsistent with current understanding (Nelson et al., *in review*), and there are no comparable studies for coho salmon.

1.5 Objectives and approach

The primary goals of this dissertation were to investigate the degree to which harbour seal predation may be impacting Chinook and coho salmon in the Salish Sea ecosystem, and to evaluate potential management alternatives that may promote the recovery of these valuable species. The specific objectives of my research were to: 1) evaluate evidence for an apparent statistical correlation between productivity of multiple wild Chinook salmon populations in the Salish Sea and harbour seal abundance; 2) estimate the number of juvenile Chinook and coho salmon that have been consumed by harbour seals in recent years in the Strait of Georgia, and 3) predict outcomes and quantify tradeoffs associated with two approaches to reducing the harbour seal population abundance in British Columbia, which some stakeholders favor as a means of recovering salmon populations. Resolving these questions will advance our current understanding of factors impacting marine survival of young Chinook and coho salmon in the northeastern Pacific, and will provide managers with information they need to evaluate the efficacy and feasibility of management alternatives that may facilitate the recovery of Pacific salmon stocks of high conservation concern.

In Chapter 2, I developed and compared multiple formulations of Bayesian hierarchical models to assess the support for an association between wild Chinook salmon productivity and seal density in the Salish Sea and Washington coast. Using several public resources, I compiled a dataset consisting of 20 different stocks from major Chinook-producing rivers in British Columbia and Washington State. With this information, I calculated the annual productivity (in recruits per spawner) of each cohort for each stock. Expanding on the standard Ricker model, I introduced two biotic covariates that may explain variation in Chinook salmon productivity: regional densities of harbour seals and regional abundance of hatchery-origin Chinook salmon.

While evaluating the explanatory power of changing seal density was my primary interest, increases in hatchery production of Chinook salmon have also occurred since the 1970s, so controlling for this alternative hypothesis was appropriate. In addition to these independent variables, I also tested models that explicitly accounted for spatial structure among model parameters, and for temporal autocorrelation in the error residuals. I then used the best-performing statistical model to infer how changes in both seal density and hatchery production would affect management reference points, such as maximum sustainable yield.

Chapter 3 of this dissertation used harbour seal diet data collected in the field from 2012-2014 and a predation model I developed to estimate the annual number of Chinook and coho salmon consumed during their first year at sea by harbour seals. Over 1,400 harbour seal "scats" were used to estimate the average monthly contribution of juvenile Chinook and coho salmon to the seal diet. We combined these diet proportions with a predation model that accounts for the growth and mortality dynamics of young salmon, and the monthly prey requirements of the total harbour seal population. A separate model for each prey species was then fit to yearly abundance data from trawl surveys in the Strait of Georgia, which allowed me to estimate the natural mortality rate from seal predation and other sources, including the numbers of individual fish consumed. Along with historical estimates of cohort size for each salmon species, we used the consumption rates of young salmon to estimate how much predation-related mortality has increased since the 1970s.

Finally, in Chapter 4, I developed two types of population dynamics models to serve as the "operating model" for a simulation study that compared two approaches to actively controlling the harbour seal population in British Columbia: indiscriminate lethal removals and non-lethal contraception. I fit simple logistic growth models and complex sex- and age-structured population models to abundance, harvest, and demographic data from previous studies, then compared their projections under numerous management scenarios involving lethal and non-lethal reductions in population size. I evaluated both the effort and duration of each management scenario required to reach a target abundance of 50% of the current population, which has recently been proposed by stakeholders as part of an effort to recover threatened salmon stocks.

My dissertation comprises three data chapters that improve understanding of the effects of marine mammal predation on young salmon in the northeast Pacific Ocean. Additionally, the simulation modeling approach I developed to test management scenarios that use lethal removals and contraception to control British Columbia's harbour seal population provide a general modeling framework that could be applied to future conservation problems involving aquatic or terrestrial species.

Chapter 2: Wild Chinook salmon productivity is negatively related to seal density and not related to hatchery releases in the Pacific Northwest

2.1 Summary

Predation risk and competition among conspecifics significantly affect survival of juvenile salmon, but are rarely incorporated into models that predict recruitment in salmon populations. Using densities of harbour seals (*Phoca vitulina*) and numbers of hatchery-released Chinook salmon (*Oncorhynchus tshawytscha*) smolts as covariates in spatially structured Bayesian hierarchical stock‑recruitment models, we found "significant" negative correlations between seal densities and productivity of Chinook salmon for 14 of 20 wild Chinook salmon populations in the Pacific Northwest. Changes in numbers of seals since the 1970s were associated with a 74% decrease (95% CI: −85%, −64%) in maximum sustainable yield in Chinook salmon stocks. In contrast, hatchery releases were significantly correlated with Chinook salmon productivity in only one of 20 populations. Our findings are consistent with recent research on predator diets and bioenergetics modeling that suggest there is a relationship between harbour seal predation on juvenile Chinook salmon and reduced marine survival in parts of the eastern Pacific. Forecasting, assessment, and recovery efforts for salmon populations of high conservation concern should thus consider including biotic factors, particularly predator-prey interactions.

2.2 Introduction

The abundance of predators and intensity of competition within a spatial arena give rise to risks associated with foraging activities that may ultimately affect the survival rates of juvenile fish (Chapman 1966; Walters and Juanes 1993; Walters and Korman 1999). When food is scarce, due to poor environmental conditions or large numbers of competitors, young fish must spend more time actively foraging, which increases their risk of being preyed upon (Walters and Juanes 1993; Ahrens et al. 2012). Physical and environmental factors often mediate these trade-offs between growth and predation risk (Friedland et al. 1993; Linehan et al. 2001; Lee et al. 2016; Andersson and Reynolds 2017), which may explain why strong, enduring correlations between recruitment and any one factor are rarely observed (Walters and Collie 1988; Bradford et al. 1997).

Many studies have attempted to explain recruitment in Pacific salmon populations via environmental (abiotic) covariates in the marine life-history stages (Beamish and Bouillon 1993; Coronado and Hilborn 1998; Beamish et al. 2000b; Sharma et al. 2013). However, fewer stock-recruitment analyses have incorporated biological covariates with mechanistic explanations such as competition, disease, and predation that influence numbers of returning salmon (Beamish et al. 2000a; Ruggerone and Goetz 2004; Ruggerone and Connors 2015). Incorporating such biotic factors (e.g., abundance of hatchery produced smolts, and densities of predating harbor seals) may improve predictions as well as provide a means to assess their impact on salmon populations of high conservation concern. This could be particularly relevant for Chinook salmon (*Oncorhynchus tshawytscha*) populations for which recruitment data have been compiled for several decades.

Marine survival rates of many Chinook salmon populations in the eastern Pacific have declined considerably since the 1970s, particularly in the inland waters of the Salish Sea (Beamish et al. 1995; Neville et al. 2015; Ruff et al. 2017). Concurrently, harbour seal (*Phoca vitulina*) populations along the west coast of North America have grown rapidly following federal protection from hunting and culling in Canada and the United States (Jeffries et al. 2003;

Brown et al. 2005; Olesiuk 2010). In the Strait of Georgia in southern British Columbia, the population of harbour seals has increased from a few thousand animals in the late 1960s to nearly 40,000 in 2008, and appears to have stopped growing (Olesiuk 2010). Further south, in Puget Sound, seal populations have seen similar seven-fold increases in abundance (Jeffries et al. 2003).

The importance of adult salmon to the diet of harbour seals has been recognized for some time (Olesiuk et al. 1990; Howard et al. 2013). Harbour seals have also been known to target out-migrating smolts in some areas of the Strait of Georgia (Olesiuk et al. 1995; Yurk and Trites 2000), but were not thought to cause significant mortality until recently (Thomas et al. 2017). Some biologists now suspect there may be a causal relationship between harbour seal predation on smolts and the low marine survival rates of some salmon and steelhead populations (Berejikian et al. 2016; Chasco et al. 2017a, b; Thomas et al. 2017).

In addition to the effects of predation on salmonids, there is a substantial literature on the deleterious effects of hatchery supplementation on wild populations of salmon in the eastern-Pacific (Naish et al. 2007). However, the majority of research on the effects of hatcheries has focused on interactions between wild and hatchery populations in freshwater (Quinn 2011), and the genetic consequences of hatchery supplementation (e.g., decreased fitness, reductions in effective population size, and weakened portfolio effects) (Waples 1991; Baskett and Waples 2013; Satterthwaite and Carlson 2015). Few studies have considered interactions between wild and hatchery populations in the marine environment (Ruggerone et al. 2003; Ruggerone et al. 2010; Zhivotovsky et al. 2012), or attempted to quantify the potential impacts of hatchery fish on wild stocks of conservation concern shortly after ocean entry (Levin et al. 2001), the life-history stage that likely determines brood year recruitment for Chinook and coho salmon (Beamish et al. 2010b; Beamish et al. 2012; Neville et al. 2015).

Concern has been expressed in the past about potentially "overloading" the marine environment with hatchery fish (Healey 1980a), and the counterproductive density-dependent impacts of large hatchery releases to overall management goals (i.e., increased yield) that could pose risks to wild populations (Peterman 1978). Potential mechanisms for negative interactions between hatchery and wild populations in the early marine stages include increased competition when foraging (Walters and Juanes 1993), or a change in the functional response that results in increased predation rates (Peterman and Gatto 1978). After nearly four decades of annual releases in the tens of millions of Chinook salmon smolts, many of the ecological tradeoffs associated with hatchery supplementation remain unclear (Naish et al. 2007), and some have questioned whether the marginal gain from hatchery releases is worth the removal of the wild fish that would sustain hatchery production (Levin et al. 2001; Beamish et al. 2012).

We sought to assess the potential impacts that harbour seal predation and hatchery releases have on wild Chinook salmon productivity, and how these vary spatially among Chinook salmon populations in British Columbia and Washington State. We did so using Bayesian hierarchical models applied to 20 individual salmon populations from the Salish Sea and Washington coast and used the best-performing model to identify potential spatial patterns and infer the strength of the relationships between productivity and the covariates. We then used the model to simulate Chinook salmon productivity over a range of combinations of seal densities and hatchery abundances to assess whether predation by seals and competition with hatchery-released fish may negatively affect the sustainable harvest of Chinook salmon.

2.3 Methods

2.3.1 Chinook salmon life-cycle

Wild Chinook salmon originating from watersheds in the Salish Sea and Washington coast spend 0-1 years in freshwater before migrating to the ocean to rear for 1-5 years, typically between the months of February and June. Juveniles that migrate to the sea after a brief freshwater residency (< 1 year) are known as "ocean-type" or "sub-yearling" fish, while populations with extended fresh water residency (at least one year) are termed "stream-type" or "yearling" fish (Quinn 2011). Fish exhibiting an ocean-type life history typically return to spawn in natal streams between August and October, and are known as "fall" Chinook salmon. Mature stream-type Chinook salmon enter natal streams as early as April. Ocean-type Chinook salmon far outnumber stream-type Chinook salmon in both wild and hatchery populations in the Salish Sea and Washington Coast. Chinook salmon are semelparous and die within weeks of spawning.

2.3.2 Salmon data

We used data published by the Pacific Salmon Commission (PSC), an international body mandated to implement the Pacific Salmon Treaty between the United States and Canada (www.psc.org). The PSC analyzes technical information from both countries and provides recommendations pertaining to fisheries management, run forecasting, and enhancement operations. Specifically, we used time-series of wild Chinook salmon escapements, brood year exploitation rates, and terminal catches (PSC 2015a, b, 2016) (Table 2.1). Wild Chinook salmon from the Salish Sea and coastal stocks are captured in a large marine mixed-stock fishery that targets both wild and hatchery fish. However, due to the high conservation concern surrounding some wild stocks, hatchery fish are marked by adipose fin clips, which allow them to quickly be distinguished from wild fish. Hatchery fish are often implanted with coded-wire tags, which (when recovered in the fishery) allows estimation of exploitation rates on a stock-by-stock basis. Often, these exploitation rates are used as a proxy for harvest rates of wild stocks (PSC 2015a, b). In this analysis, we only included wild stocks where the exploitation rates were believed to be comparable between wild and hatchery populations originating from the same river. Upon returning to their natal streams, wild fish are counted on their spawning grounds using a variety of methods (also described in PSC 2015a, b, 2016). These methods include aerial surveys, mark-recapture studies, snorkel surveys, etc. Hatchery-origin fish are collected at the hatchery, although fish are known to stray to wild populations (Naish et al. 2007).

Table 2.1: Summary of information used to compile spawner-recruit data for 20 stocks of wild fall Chinook salmon in British Columbia and Washington State. Included in the table are population regions: Strait of Georgia (SOG); Puget Sound (PS); Strait of Juan de Fuca (JDF), and Washington Coast (WA Coast). Also provided are the number (n) and range of brood years for each population in the stud, in addition to the source of the data.

Stock No.	Stock Name	Region	n	Brood Years (range)	Sources
1	Cowichan River	SOG	23	1985-2008	1, 2, 3
2	Puntledge River	SOG	33	1975-2008	1, 2, 4, 5
3	Nanaimo River	SOG	19	1979-2004	1, 2, 6
4	Quinsam River	SOG	31	1976-2007	1, 2, 7
5	Big Qualicum River	SOG	36	1973-2008	1, 2, 4, 8
6	Harrison River (Fraser)	SOG	24	1984-2008	1, 2, 4, 8
7	Shuswap River (Fraser)	SOG	25	1984-2008	1, 2, 4, 8
8	Chilliwack River (Fraser)	SOG	28	1981-2008	1, 2, 4, 8
9	Skokomish River	PS	29	1972-2006	1, 2, 9, 10
10	Skagit River	PS	26	1983-2008	1, 2, 10
11	Snohomish River	PS	27	1980-2007	1, 2, 10
12	Stillaguamish River	PS	23	1980-2007	1, 2, 10
13	Green River	PS	31	1975-2007	1, 2, 10
14	Lake Washington	PS	31	1975-2007	1, 2, 10
15	Nisqually River	PS	28	1979-2006	1, 2, 10
16	Hoko River	JDF	20	1986-2006	1, 2, 10
17	Elwha River	JDF	7	1986-1994	1, 2, 10
18	Queets River	WA Coast	29	1977-2006	1, 2, 8
19	Quillayute River	WA Coast	26	1980-2006	1, 2, 8
20	Hoh River	WA Coast	29	1977-2006	1, 2, 8

Sources: 1, PSC (2015a, b); 2, PSC (2016); 3, Tompkins et al. (2005); 4, NuSEDS Database (via www.npafc.org); 5, Trites et al. 1996; 6, Lam and Carter (2010); 7, Bennett et al. (2010); 8, NMFS (1997); 9, www.streamnet.org; 10, WDFW (2010).

Some datasets—specifically, the escapements of non-indicator stocks—were augmented by the Salmon Escapement Database (NuSEDS) managed by Canada's Department of Fisheries and Oceans (DFO) (DFO 2016), and the StreamNet database managed by the Pacific States Marine Fisheries Commission (PSMFC) (www.streamnet.org).

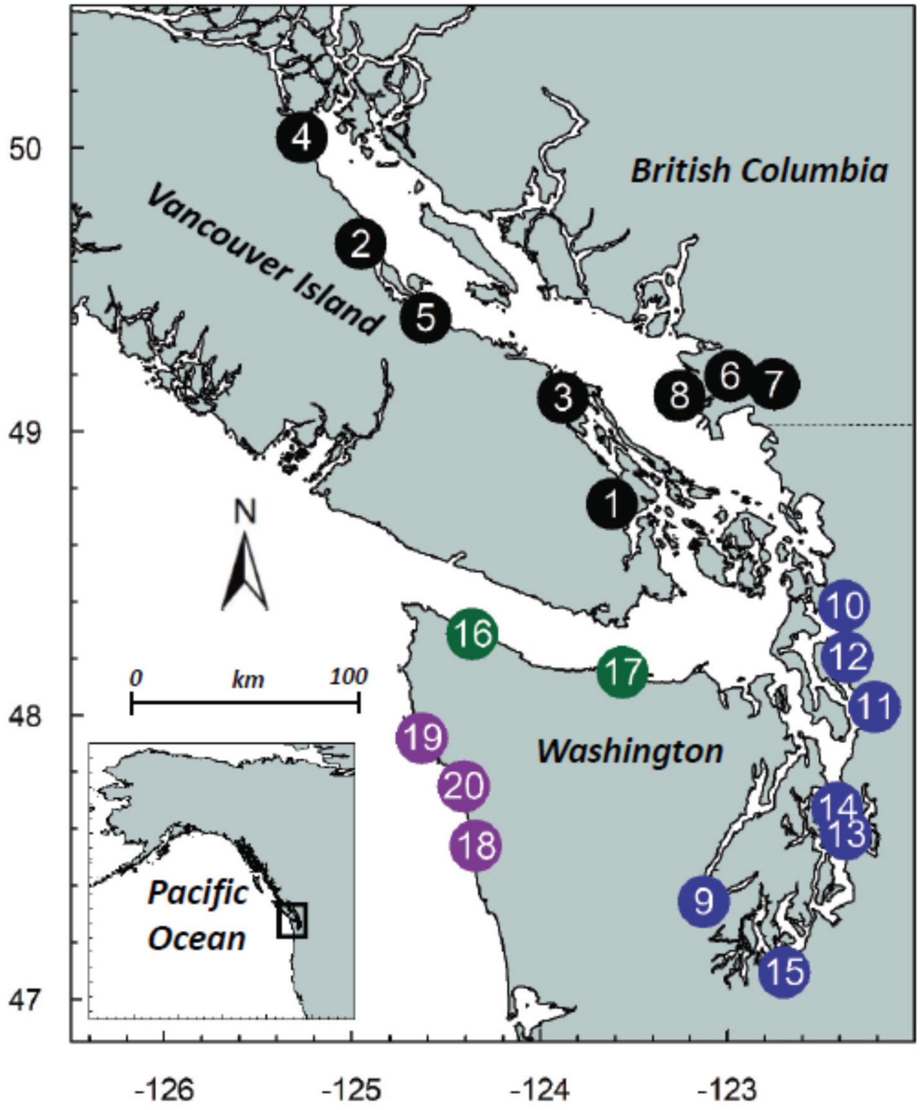

Figure 2.1: The study area showing locations of the 20 Chinook salmon populations in British Columbia and Washington State included in the analysis. Numbers correspond to the population information and data summaries shown in Table 2.1. Map data: Schnute (2017); Wessel and Smith (1996).

Spawner-recruit data were compiled for 20 individual stocks (N=20) of fall Chinook salmon from British Columbia and Washington State (Table 2.1; Fig. 2.1). Because seal predation rates on salmon smolts may vary according to the body size of their prey (Thomas et al. 2017), we controlled for size-related predation effects by restricting our analysis to populations that exhibit an "ocean-type" life-history, where juvenile freshwater residency is less than one year (i.e., "sub-yearlings"). Limiting our analysis to "ocean-type" Chinook salmon also minimized the possibility of capturing density-dependent effects of hatchery abundance in freshwater, which are believed to be minimal due to the very short residency period. We used a cohort reconstruction approach to calculate the number of recruits produced in each brood year (the calendar year when parents spawned) from the escapement and catch data (Fleischman et al. 2013). Pre-fishery recruitment (ocean age-2) for each brood year (R_t) was calculated by adding the total run (N_t) to the number of individuals harvested in ocean and terminal fisheries, which was derived from the stock-specific brood year exploitation rates (U_t) provided by the PSC (PSC 2015a, b):

(Eq. 2.1)

$$R_t = \frac{N_t}{(1 - U_t)}$$

where the total run (N_t) is the sum of spawning adults from the same brood year t across multiple ages (a):

(Eq. 2.2)

$$N_t = \sum_{a=2}^{5+} S_{t+a,a}\, p_{t+a,a}$$

and $S_{t+a,a}$ is the number of observed spawners in calendar year $t + a$, and $p_{t+a,a}$ are the proportions of spawners at age a in that calendar year. Because age-at-maturity can be highly variable for Chinook salmon (mature at 2-7 years), age composition from coded-wire tag data gathered on the spawning grounds is necessary to assign escaped fish to brood year. These data were compiled from various resources that were publicly available (see: Table 2.1). For many stocks, age-composition data were not available for every year. In these instances, we used the mean age-composition calculated from years where data were available to complete the cohort reconstruction.

Annual hatchery releases of fall Chinook salmon in each region of British Columbia and Washington State (i.e., Strait of Georgia, Puget Sound, Washington Coast) were summarized using data from the North Pacific Anadromous Fish Council (NPAFC) (http://www.npafc.org/new/science_statistics.html) (NPAFC 2016), technical documents published by the PSC (PSC 2016), and the Regional Mark Information System database (http://www.rmpc.org, accessed 25 February 2017) (Fig. 2.2).

2.3.3 Harbour seal densities

We used published estimates of harbour seal abundances from aerial surveys to estimate predator densities by region (i.e., seals/km of shoreline). Regional seal densities were calculated by dividing the total annual abundance in each region by the lengths of shorelines in the corresponding region (Fig. 2.2; Table 2.2). A time-series of harbour seal abundances in the Strait of Georgia was available from DFO's published aerial survey data (Olesiuk 2010), and estimates of harbour seal abundance in the Puget Sound, Washington coast, and Strait of Juan de Fuca were available from Jeffries et al. (2003). In both British Columbia and Washington, abundance estimates were not available every year—typically every 2-3 years. We thus fit autoregressive state-space models to survey data published by Jeffries et al. (2003) and Olesiuk (2010) to impute abundances for years when surveys were not conducted (see: Appendix A).

Table 2.2: Summary of information used to calculate time-series of harbour seal densities in each region in British Columbia and Washington State. Using 2008 as an example, this includes the annual estimate of abundance and an estimate of shoreline length in each region. The Chinook salmon populations associated with each region are listed in the last column.

Region	Estimated 2008 Abundance	Shoreline length (km)	2008 Density	Chinook Populations (Table 2.1)
Strait of Georgia	37,552	2,965	12.7	1-8
Puget Sound	15,032	2,144	7.0	9-15
Juan de Fuca	2,704	225	12.0	16-17
Washington Coast*	7,019	224	31.3	18-20

* Includes Washington coastal shoreline north of Grays Harbor and south of Neah Bay, which coincides with the "Olympic Peninsula" region delineated in Jeffries et al. (2003).

2.3.4 Modeling approach

The Chinook salmon spawner-recruit datasets were assembled with the seal density and hatchery release data described above, and Bayesian regression models were used to assess how each factor, or combination of factors, may have affected productivity since the 1970s. We evaluated 144 candidate models, using different model structures (non-hierarchical vs. hierarchical, non-spatial vs. spatial), covariates (seal density, hatchery releases), and assumptions. Our modeling approach used the Ricker stock-recruitment relationship (Ricker 1954) as a base model to account for intra-population density-dependent impacts on productivity:

(Eq. 2.3) $$R_{i,t} = S_{i,t}e^{(\alpha_i - \beta_i S_{i,t} + \varepsilon_{i,t})}$$

where $R_{i,t}$ is the number of recruits produced from the spawners $S_{i,t}$ in brood year t for stock i (i = 1,…, N); α is the productivity parameter, β is the density-dependent parameter (Quinn and Deriso 1999), and ε_t are the error residuals, which are assumed to be normally distributed $Normal(0, \sigma_i^2)$.

We used the Ricker stock-recruitment relationship here because it is conveniently linearized (from Eq. 2.3) to enable evaluation of additional covariates (Hilborn and Walters 1992). Additionally, the Ricker formulation allows for the possibility of reduced productivity at high spawner abundances (Ricker 1954):

(Eq. 2.4)

$$ln\left(\frac{R_{i,t}}{S_{i,t}}\right) = \alpha_i - \beta_i S_{i,t} + \varepsilon_{i,t}$$

In the base model, stock-specific parameters (α_i, β_i and σ_i^2) are estimated separately and without additional covariates. Temporal autocorrelation was accounted for by modeling the error residuals as an AR(1) process: $\varepsilon_{i,t} = \rho_i \varepsilon_{i,t-1} + \delta_{i,t}$, where $\delta_{i,t} \sim Normal(0, \sigma_i^2)$. The AR(1) process was omitted from the model during the first brood year of the time-series, and in brood years where data from the preceding year was not available.

To infer the potential effects of harbour seal predation and hatchery releases on stock productivity we introduce two covariates to Eq. 2.4:

(Eq. 2.5)

$$ln\left(\frac{R_{i,t}}{S_{i,t}}\right) = \alpha_i - \beta_i S_{i,t} + q_i \text{Seal}_{j,t+1} + h_i \text{Hatch}_{k,t+1} + \varepsilon_{i,t}$$

where q_i is the coefficient associated with harbour seal density near stock *i*, in region *j*, in year *t+1* ($\text{Seal}_{j,t+1}$), which is lagged one year to coincide with the salmon cohort's first year at sea. The coefficient h_i relates productivity to the number of hatchery conspecifics released in region *k* ($\text{Hatch}_{k,t+1}$), and is also lagged to correspond to ocean entry timing of smolts from stock *i*. Prior to fitting the models we re-scaled the values of both independent variables for more efficient computation: (Hatch x 10^{-7}), (Seal x 10^{-1}).

2.3.5 Hierarchical and spatially correlated prior distributions

We evaluated two types of hierarchical priors on α_i, q_i, and h_i parameters in full and nested versions of Eq. 2.5. The first was a conventional prior that assumed an exchangeable distribution where the stock-specific parameters arise from a common distribution (e.g., $q_i \sim Normal(\mu_q, \tau_q^2)$). This approach is used frequently in stock-recruitment modeling of salmon populations (Su et al. 2001; Michielsens and McAllister 2004; Liermann et al. 2010), and has the advantage of allowing data-poor stocks to “borrow strength” from those with more informative data. This can lead to more precise estimates of the individual parameters and “shrinkage” of the parameter estimates around a global mean. Non-informative priors were assigned to both the mean (e.g., $\mu_q \sim Normal(0, 10^5)$) and variance (e.g., $\tau_q^2 \sim \mathrm{IG}(0.01, 0.01)$) hyper-parameters for α_i, q_i, and h_i, where IG is an inverse gamma distribution (Su et al. 2001; Su et al. 2004). We also evaluated models with variance hyper-parameters of IG(0.001, 0.001) and found no meaningful differences in parameter estimates.

The second hierarchical prior we evaluated was a spatially correlated Gaussian conditional autoregressive (CAR) prior (Su et al. 2004). Similar formulations of CAR priors are widely used in medical and epidemiological studies, particularly for disease mapping (Carlin and Banerjee 2003; Jin et al. 2005). The spatially correlated prior allows values for individual parameters for those populations in close proximity (e.g., α_i, q_i, and h_i) to cluster, thereby capturing the dynamics that may be unique to a specific region. For instance, it is well documented that variation in migration routes (i.e., different ocean entry points) can result in different survival rates for several species of Pacific salmon (Melnychuk et al. 2010; Welch et al. 2011; Furey et al. 2015; Moore et al. 2015; Healy et al. 2017). We hypothesize that encounter rates with predators and conspecifics (competition, disease, etc.) could be a function of where smolts commence their marine migrations.

As an example, the formulation of the CAR prior used on q_i, conditional on the parameters at other locations (q_i given $q_j, j \neq i$), is:

(Eq. 2.6)
$$q_i | q_j, j \neq i \sim Normal\left(\frac{\sum_{j \neq i} \varphi_{i,j} q_j}{\sum_{j \neq i} \varphi_{i,j}}, \frac{\tau_q^2}{\sum_{j \neq i} \varphi_{i,j}}\right); i, j = 1, \dots, N$$

where $\varphi_{i,j}$ is the influence of q_j on q_i, and τ_q^2 is the variance parameter. When employing a CAR model, a neighborhood structure needs to be specified to facilitate inference about the spatial relatedness among individual parameters (Rodrigues and Assunção 2012). The “neighborhood” for our analysis consisted of a matrix of pairwise distances between populations i and j, which we defined as the approximate over-water distance (in km) between the ocean entry points of each population. More specifically, this is the shortest hydrologic distance (i.e. not crossing over land) between the terminuses of the two individual rivers associated with each population. We assumed an exponential relationship (Su et al. 2004; Ward et al. 2015)

(Eq. 2.7)
$$\varphi_{i,j} = exp\left(-d_{i,j} \omega_q\right)$$

where $d_{i,j}$ is the inter-population spatial distance, and ω_q is an estimated parameter that quantifies the degree of spatial relatedness among individual q’s. Very small values of ω_q would suggest an exchangeable model where individual parameter values are not dependent on spatial proximity, while large values would suggest parameters that are fully independent from others (also unrelated spatially). Alternatively, moderate values would indicate clustering towards a local average. Similar to Su et al. (2004), we assigned uniform priors to ω_α, ω_q, and ω_h, using a lower bound of zero and an upper bound of 2. This interval was determined to cover all plausible values of the ω parameters. We assessed sensitivity to the prior for ω using the alternative distributions U(0, 5) and U(0, 10), and concluded there was no discernable difference in model output or performance.

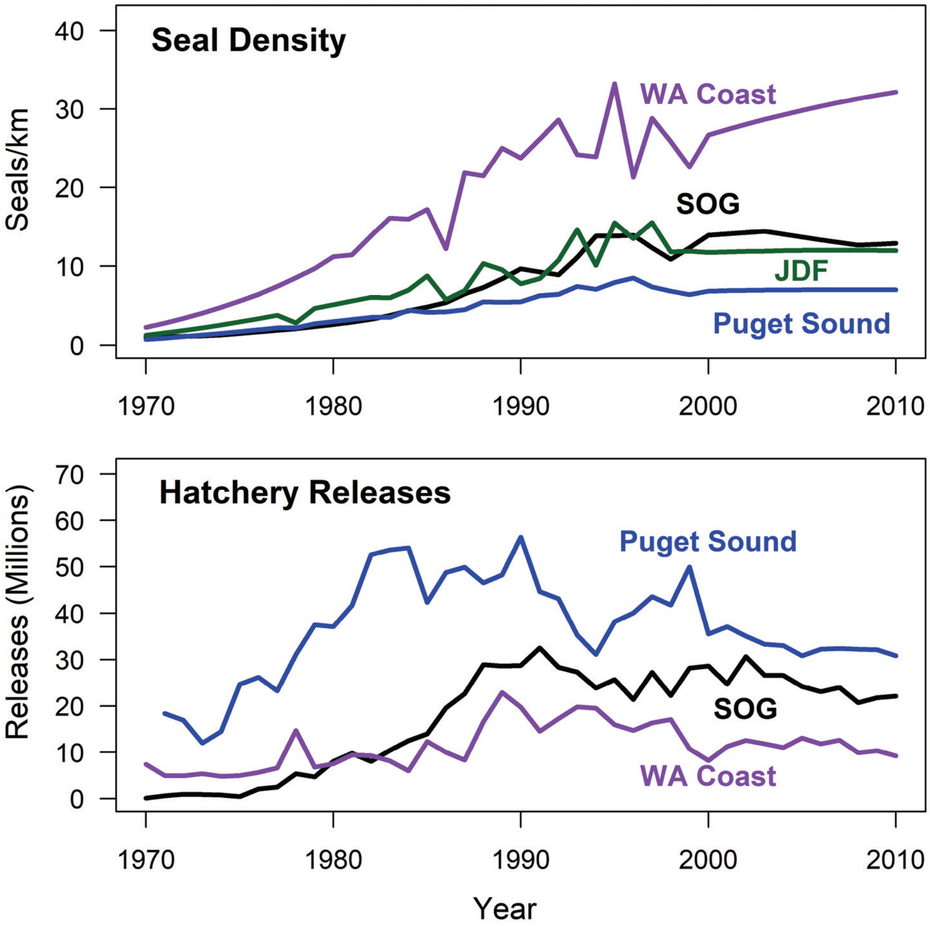

Figure 2.2: Time-series of harbour seal densities (top panel) and hatchery releases (bottom panel) of fall Chinook salmon in each region between the 1970s through 2010. Geographic regions include: Strait of Georgia (SOG), Puget Sound, Juan de Fuca (JDF), and Washington Coast (WA Coast).

2.3.6 Other prior distributions

For all models, we assigned non-informative prior distributions to the stock-specific parameters β_i and σ_i^2: β_i~*Normal*(0, 10^5) and σ_i^2~IG(0.01, 0.01) (Su et al. 2004). In models where α_i, q_i, or h_i were fixed effects, we also imposed non-informative priors on the coefficients in the form of a normal distribution with a mean of zero and a large variance: e.g., α_i~*Normal*(0, 10^5).

2.3.7 Multicollinearity in the independent variables

Harbour seal density and hatchery releases of fall Chinook salmon exhibit similar increasing trends since 1970 in some regions (Fig. 2.2), so we assessed multicollinearity for combinations of independent variables in all 20 populations (Zar 2009). Variance Inflation Factors (VIFs) were calculated for each independent variable included in the model: $VIF_k = (1 - R_k^2)^{-1}$, where R_k^2 is the coefficient of determination for the linear regression where the *kth* independent variable is a function of the remaining independent variables. The VIF quantifies the increase in variance of a regression coefficient due to collinearity among the independent variables. VIFs of 10 or above are indicative of pathological multicollinearity, which requires re-evaluating the choice of independent variables included in the model (Hair et al. 2010), while a VIF of 1 would indicate no correlation among independent variables. We also calculated correlation coefficients for each combination of parameters associated with the independent variables (spawners [Ricker b], seal densities [q], and hatchery abundance[h]) for the best performing model. If collinearity exists between independent variables, the level of correlation between their associated parameters may be high.

2.3.8 Estimation of reference points (U_{MSY} and MSY)

One of the most appealing features of the Ricker equation (Eqs. 2.3 and 2.4) is the availability of precise analytical approximations for biological and management reference points (Hilborn and Walters 1992): a stock's maximum sustainable yield (MSY); the harvest rate that produces MSY (U_{MSY}); the number of spawners required to produce MSY (S_{MSY}), and the size of the spawning stock that yields the most recruit production (S_{MSR}). However, because of the complex age and maturation patterns of Chinook salmon (2-7 years), and the relatively high number of pre-fishery age-2 recruits (indicated by large values of α in Eq. 2.3) (Fleischman et al. 2013), we computed U_{MSY} and MSY using equilibrium yield calculations detailed in Appendix A. For each stock, we computed U_{MSY} and MSY at different combinations of seal densities and hatchery abundances to evaluate the implications of both covariates on levels of sustainable harvest.

2.3.9 Bayesian computation

Bayesian inference was performed using WinBUGS software (Spiegelhalter et al. 1996) via the "R2WinBUGS" package (Sturtz et al. 2005) in the R Programming Environment (R Core Team, 2014). For each candidate model, we generated three separate Markov Chain Monte Carlo (MCMC) chains of 100,000 iterations per chain and discarded the first half of each (50,000). The remaining samples were used to calculate posterior means, standard deviations, medians, and quantiles for all parameters and quantities of interest. We assessed model convergence by visual inspection of trace plots, and evaluation of Gelman-Rubin diagnostic statistics (R-hat) for each model parameter (Gelman et al. 2013).

2.3.10 Model comparison and posterior predictive checking

To compare the within-sample predictive accuracy of candidate models in the analysis, we calculated their deviance information criterion (DIC), which is often used to evaluate Bayesian models with hierarchical structure (Ward 2008; Gelman et al. 2013). A difference of at least two DIC units (ΔDIC) would indicate a significant difference in performance between two competing models (Spiegelhalter et al. 2002). We also used the posterior predictive distributions to evaluate the ability of our best performing model to replicate the observed data (Gelman et al. 2013). This was achieved by calculating the proportion of data points captured by the 95% posterior predictive intervals, and by graphically displaying the observed data alongside the simulated data (i.e., the 95% posterior predictive intervals) to see if any observable patterns or systematic differences existed between the observed and predicted values. Additionally, to assess the goodness-of-fit of the best performing model, we calculated its posterior predictive p-value (Meng 1994; Gelman et al. 2013). We used the chi-squared discrepancy measure as a test statistic (T) to compare observed and simulated data:

(Eq. 2.8)

$$\chi^2: T(y, \theta) = \sum_{i=1}^{n} \frac{[y_i - E(Y_i|\theta)]^2}{VarE(Y_i|\theta)}$$

where y_i is the observed (or simulated) data, and $E(Y_i|\theta)$ is the expected value, which is a function of the data and the parameters (θ).

2.4 Results

2.4.1 Bayesian computation and posterior predictive checking

Convergence diagnostics and predictive checking did not suggest any problems associated with autocorrelation in the MCMC chains, convergence, or model fit (Appendix A).

2.4.2 Multicollinearity in the independent variables

Of the 60 combinations of independent variables (20 populations x 3 variables) used in the candidate models, none exhibited serious levels of multicollinearity (VIF > 10) (Table A1). Only one of the variables (seal density, Puntledge River population) had an intermediate VIF of 4.27. The mean VIF (weighted by the sample size of each dataset) was 1.89 for seal density, 1.27 for hatchery abundance, and 1.86 for spawner variables across study populations (Table A1). In addition, the correlation coefficients of the parameter combinations for the best model (Model 1) only showed low to moderate levels of correlation (Appendix A, Table A2).

2.4.3 Model comparison

According to our model selection criteria (described in the previous section), candidate models that assumed a common variance among stocks performed much more poorly than identical models with a unique variance for each stock (σ_i^2). Additionally, models that accounted for temporal autocorrelation by assuming error residuals follow a first-order autoregressive process (AR[1]) outperformed identical models without this assumption. Therefore, in the following sections we only present the results for the 48 models that assumed a stock-specific variance term and temporal autocorrelation in those terms.

Several notable outcomes arise from comparing the 48 candidate models. The most obvious and important result is that the models incorporating regional seal density as a covariate performed far better than those that did not (Table 2.3; Fig. 2.3). The top hierarchical (Model 1) and non-hierarchical models (Model 23) out-performed their counterparts that omitted a seal covariate by a wide margin (Table 2.3 and Fig. 2.3). The disparity in DIC between the lowest ranked model that included a seal covariate (Model 36) and the highest ranked model that omitted the seal covariate (Model 37) is substantial (ΔDIC=90). The highest ΔDIC between models that included a seal covariate is only DIC 25 units (Fig. 2.3). The best-performing model is a hierarchical model (Model 1) that estimated stock-specific α_i parameters separately and drew seal-associated coefficients q_i from a common distribution (i.e., they were exchangeable). Both models with a ΔDIC ≤ 2 include a hierarchical prior on q_i without spatial structure (Models 1 and 2).

The second important finding from model comparison was the relatively small improvement in model performance gained by including a covariate for regional annual hatchery abundance (Fig. 2.3). Of the top 36 models that contained a covariate for seal density (Models 1-36), 27 of them included hatchery covariates (Table 2.3). The top five models according to DIC (Models 1-5) included hierarchical priors on h_i, but the added complexity was not a meaningful improvement over the next highest rated model (Model 6), which had a ΔDIC ≤ 2. Both of the top-tier models (ΔDIC ≤ 2) included a covariate for hatchery abundance.

Accounting for spatial correlations among stock-specific covariates did not significantly improve model performance (Table 2.3). Only one of the top-tier models (Model 2) included spatial structure using the CAR prior (on the h_i coefficient). The most complex candidate models evaluated (number of parameters >124), imposed exchangeable or spatially structured priors on three coefficients (α_i, q_i, h_i), and were outperformed by models that had no hierarchical structure (Model 17) (Table 2.3). However, there was a positive correlation between model complexity and performance and ranking (Table 2.3). For example, the top models all had at least 100 parameters, while the worst performing model (Model 48), the basic Ricker, had the fewest parameters (60). As intended, hierarchical models facilitated borrowing of information, as suggested by the lower number of effective parameters (pD) compared to the actual number of model parameters (Np) in all cases (Table 2.3). Conversely, the non-hierarchical models had numbers of effective parameters that were close to or even exceeded the number of actual parameters (e.g., Models 17 and 48; Table 2.3).

2.4.4 Effect of seal density

The mean seal density coefficient (q) for the best performing model (Model 1, exchangeable prior on q) was -0.96 (95% CI: -1.39, -0.57) and had a very high probability of being negative (> 99%). In addition, the individual posterior means (q_i) were negative for 19 of 20 populations (Table 2.4), and 14 of those populations had 95% posterior credible intervals that did not overlap with zero (Table 2.4 and Fig. 2.4). Regions where there was a high probability (>95%) of a negative q_i included the central Puget Sound (Snohomish, Stillaguamish, Green, and Lake Washington), east Vancouver Island (Cowichan, Nanaimo, Quinsam, Qualicum), and the Washington coast (Queets, Quillayute, Hoh) (Table 2.4). The only populations where the probability of a negative q_i was less than 90% included the Puntledge (73%) and Shuswap (87%) in the Strait of Georgia, the Nisqually (87%) in the Puget Sound, and the Hoko (45%) in the Strait of Juan de Fuca (Table 2.4).

2.4.5 Effect of hatchery releases

The mean coefficient for hatchery releases (h) for the top-ranked model (DIC) (Model 1, exchangeable prior on h) was 0.00 (95% CI: -0.12, 0.12) and had a 48% probability of being negative. Ten of the stock-specific coefficients h_i had posterior means with negative values. However, 19 of the 20 coefficients had posterior credible intervals that overlapped with zero (Table 2.4). The Stillaguamish River in the central Puget Sound was the only stock whose posterior distribution of h_i did not overlap with zero (Table 2.4). Several populations in the analysis had a high (but not statistically significant) probability of a negative h_i parameter: Nanaimo (80%), Lake Washington (88%), and Queets (89%) (Table 2.4).

No spatial patterns were apparent when examining the individual h_i parameters generated by the best-performing model (Model 1) (Table 2.4; Fig. 2.4). Furthermore, the second ranked model by DIC (Model 2), which performed virtually the same as the highest ranked model (ΔDIC=2), included a CAR prior on h_i with a posterior mean of 0.03 (95% CI: 0.00, 0.09) for ω_h. The mean value implies populations separated by less than approximately 23 km have correlated h_i parameters (assuming a correlation of 0.50, using Eq. 2.7). However, the wide credible intervals associated with this parameter preclude making any strong conclusions regarding the spatial relatedness of hatchery effects.

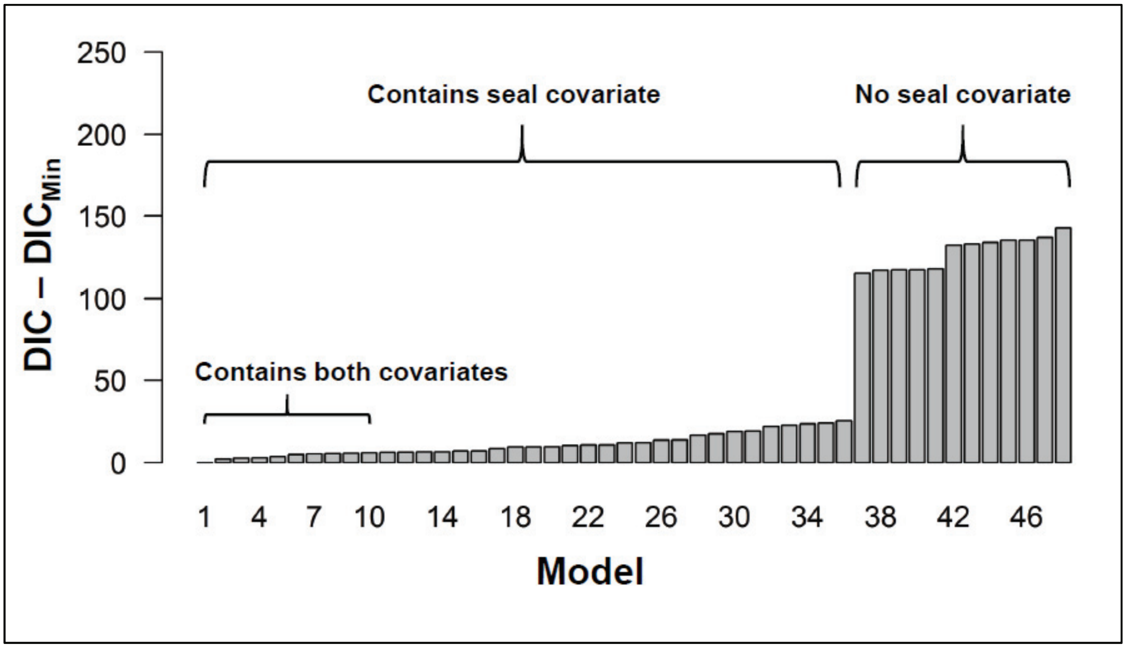

Figure 2.3: The top 48 candidate models for 20 Chinook salmon stocks ranked according to their deviance information criterion (DIC). The y-axis unit is the model DIC minus the lowest DIC among all candidate models. Model numbers are on the x-axis and correspond with model structures shown in Table 2.2. Models 1-10 contain both seal and hatchery covariates. Models 1-36 contain the seal covariate, while Models 37-48 do not.

Table 2.3: Model selection criteria for the top 30 candidate models (Models 1-30), the highest ranked model not including seal density (Model 37), and the least credible model overall (Model 48). Coefficients with spatially structured CAR priors are denoted CAR; coefficients with exchangeable hierarchical priors are labeled EXH; coefficients with independent estimates for each stock are denoted simply by the parameter symbols α_i, q_i, and h_i. Stock-specific β parameters were estimated individually in all candidate models. Included in the table are the number of effective parameters (pD), the total number of parameters (Np), average deviance ($\overline{D}$), total DIC, ΔDIC, and the coefficient of determination (R-squared).

Model	Model Structure	pD	Np	$\overline{D}$	DIC	Δ DIC	R-squared
1	α_i + EXH q_i + EXH h_i	100	124	773	773	0	0.68
2	α_i + EXH q_i + CAR h_i	102	124	673	775	2	0.68
3	EXH α_i + q_i + EXH h_i	98	124	678	776	3	0.67
4	α_i + CAR q_i + EXH h_i	99	124	677	776	3	0.67
5	CAR α_i + q_i + EXH h_i	99	124	678	777	4	0.67
6	α_i + EXH q_i + h_i	110	122	668	778	5	0.69
7	α_i + CAR q_i + CAR h_i	101	124	677	778	5	0.68
8	EXH α_i + EXH q_i + h_i	104	124	674	778	5	0.68
9	α_i + q_i + EXH h_i	106	122	673	779	6	0.68
10	CAR α_i + EXH q_i + h_i	104	124	675	779	6	0.68
11	EXH α_i + q_i	91	102	688	779	6	0.67
12	EXH α_i + q_i + CAR h_i	100	124	679	779	6	0.67
13	CAR α_i + q_i + CAR h_i	101	124	679	779	6	0.67
14	α_i + EXH q_i	90	102	689	780	7	0.67
15	CAR α_i + q_i	91	102	689	780	7	0.67
16	α_i + CAR q_i + h_i	107	122	673	780	7	0.68
17	α_i + q_i + CAR h_i	108	122	673	781	8	0.68
18	EXH α_i + EXH q_i + EXH h_i	91	126	691	782	9	0.67
19	EXH α_i + q_i + h_i	110	122	672	782	9	0.68
20	CAR α_i + q_i + h_i	111	122	672	783	10	0.68
21	EXH α_i + CAR q_i + h_i	100	124	683	783	10	0.67
22	CAR α_i + CAR q_i + h_i	101	124	683	784	11	0.67
23	α_i + q_i	97	100	687	784	11	0.67
24	α_i + CAR q_i	90	102	695	785	12	0.67
25	α_i + q_i + h_i	118	120	667	785	12	0.68
26	CAR α_i + EXH q_i + EXH h_i	91	126	696	787	14	0.66
27	EXH α_i + EXH q_i + CAR h_i	93	126	694	787	14	0.67
28	EXH α_i + EXH q_i	83	104	707	790	17	0.67
29	EXH α_i + CAR q_i + EXH h_i	85	126	705	790	18	0.66
30	CAR α_i + CAR q_i + EXH h_i	86	126	706	792	19	0.66
…							
37	α_i + EXH h_i	89	102	799	888	115	0.64
…							
48	α_i (Basic Ricker)	76	80	840	916	143	0.61

2.4.6 Management reference points

The implications of seal density and hatchery abundance on the sustainable harvest rate (U_{MSY}) and maximum sustainable yield (MSY) for each stock (Figs. 2.5 and 2.6) were based on projections using the estimated parameters from Model 1. After simulating yield over all observed levels of hatchery abundance, we estimated that changes in seal density between 1970 and mid-2000s resulted in an average decrease in MSY of -74% (95% CI: -85%, -64%) (Table 2.5). Similarly, the average decrease in U_{MSY} due to seal effects across all stocks was 44% (95% CI: -52%, -35%). With the exception of the Hoko River population, there was an inverse relationship between seal density and yield (Fig. 2.5). The most drastic reductions in yield due to seal effects were in the Cowichan River (-94%) and along the Washington Coast (Table 2.5).

The effect of hatchery releases on U_{MSY} and MSY was not nearly as consistent compared to the effect of seal density (Fig. 2.6; Table 2.5). We estimated that changes in hatchery releases between 1970 and mid-2000s resulted in an average increase in MSY of 9% (95% CI: -6%, 25%) (Table 2.5). High levels of hatchery releases were associated with increased sustainable harvest rates and yields for some populations (Fig. 2.6). The model suggests that increased hatchery abundance may buffer harvest yield against low to moderate seal densities in the Skokomish and Stillaguamish populations in the Puget Sound (Fig. 2.5). However, hatchery releases appeared to suppress the potential yield in others (Fig. 2.5-2.6). The effect of hatchery releases on U_{MSY} and MSY varied considerably, even among populations within the same geographic region. For example, on east Vancouver Island in the Strait of Georgia, high harvest rates on the Nanaimo, Quinsam and Qualicum River stocks appear to have coincided with low seal densities and low levels of hatchery production (Fig. 2.5). Conversely, harvest rates of Chinook salmon from the

Cowichan and Puntledge populations appeared to be higher when densities of seals were low and hatchery releases were high.

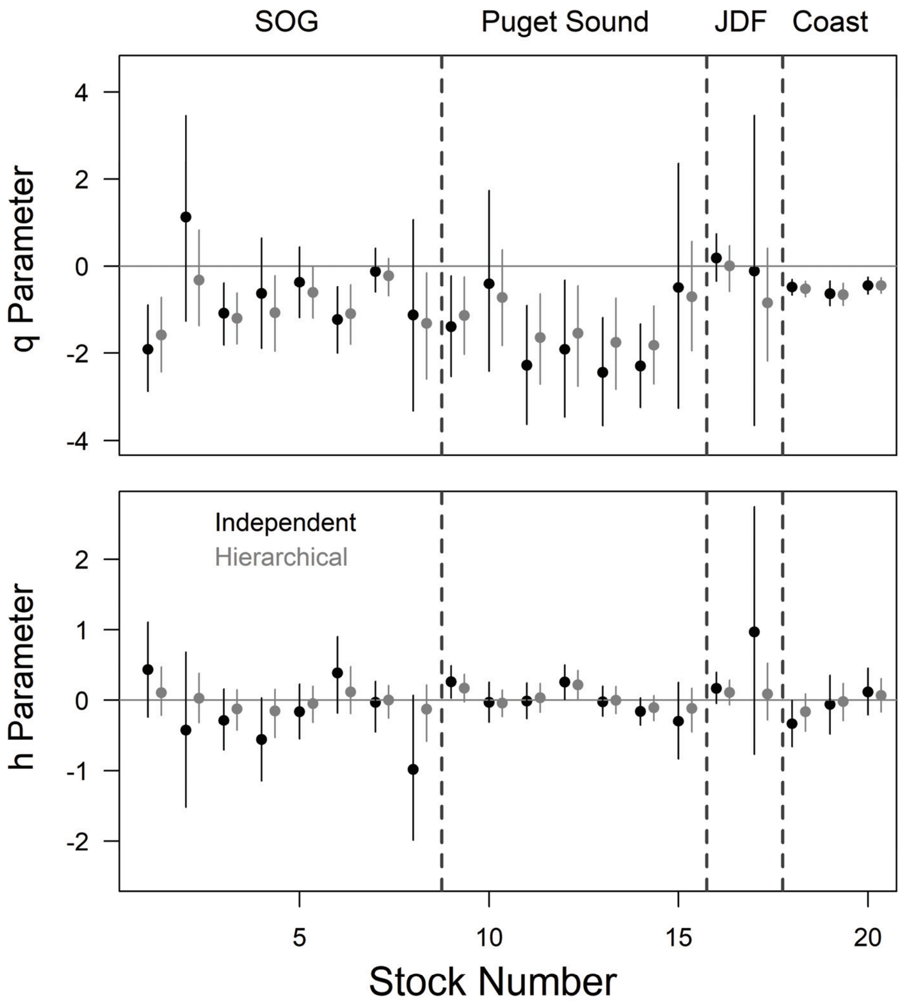

Figure 2.4: Plots of q_i (seal density coefficient, top panel) and h_i (hatchery releases coefficient, bottom panel) by Chinook salmon stock. The black series show estimates for the full non-hierarchical model (Model 25), while then grey series is the top-ranked hierarchical model by DIC (Model 1). Circles represent the posterior means and the colored lines show the 95% posterior credible intervals. The black vertical dashed lines separate the stocks by region: Strait of Georgia (SOG); Puget Sound (PS); Strait of Juan de Fuca (JDF), and Washington coast (Coast).

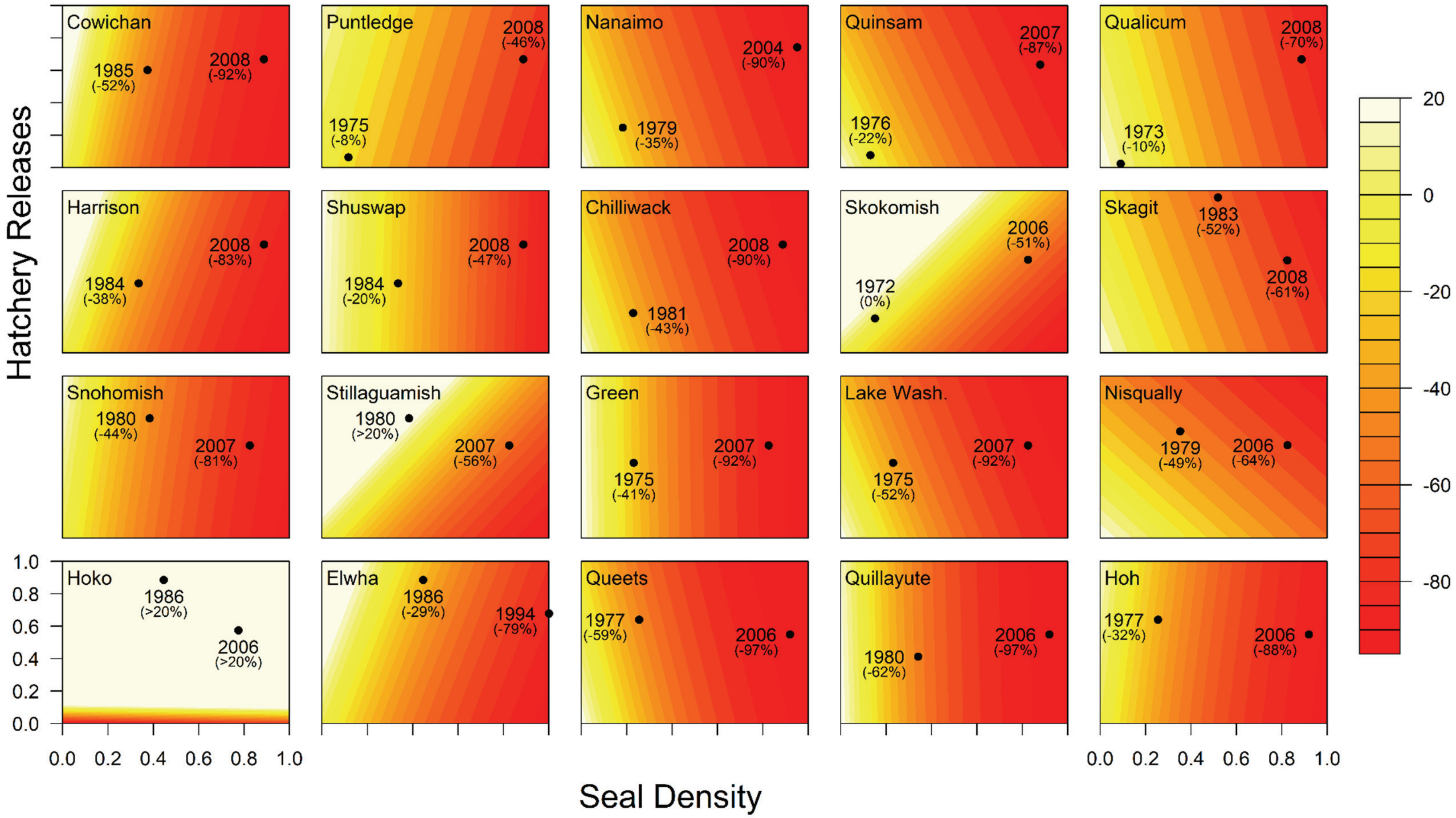

Figure 2.5: Estimated percent change in maximum sustainable yield (MSY) since 1970 over different combinations of seal densities and hatchery abundance for 20 Chinook salmon stocks. Both variables are standardized by the maximum observed value of each variable between 1970 and 2010. The predicted change in MSY for the first and last years in the dataset for each population (see: Table 2.1) are shown using black circles with the estimated percent change in MSY in parentheses.

Table 2.4: Summary of posterior distributions, by Chinook salmon stock, for parameters from the best performing model (Model 1). Posterior means and 95% credible intervals (in parentheses) are presented for each parameter. Seal density (*q*) and hatchery release (*h*) coefficients with posterior credible intervals that do not overlap with zero (i.e., are 'significant') are shown in bold. Also shown (columns 6 and 8) are the probabilities that coefficients q_i and h_i have a value less than zero.

Stock	Stock Name	Ricker α	Ricker β (x 10^3)	q	Pr (q < 0)	h	Pr (h < 0)
1	Cowichan	3.48 (2.03, 4.80)	-0.10 (-0.17, -0.03)	**-1.59 (-2.43, -0.72)**	100%	0.10 (-0.21, 0.47)	27%
2	Puntledge	2.07 (0.89, 3.27)	-0.21 (-0.35, -0.07)	-0.32 (-1.37, 0.82)	73%	0.03 (-0.32, 0.38)	44%
3	Nanaimo	4.14 (3.15, 5.12)	-0.75 (-1.06, -0.43)	**-1.20 (-1.79, -0.62)**	100%	-0.12 (-0.43, 0.15)	80%
4	Quinsam	3.87 (2.98, 4.78)	-0.33 (-0.47, -0.19)	**-1.08 (-1.96, -0.21)**	99%	-0.15 (-0.53, 0.15)	81%
5	Qualicum	3.02 (2.51, 3.51)	-0.47 (-0.60, -0.35)	**-0.61 (-1.20, -0.01)**	98%	-0.05 (-0.31, 0.20)	65%
6	Harrison	2.78 (1.67, 3.92)	-0.01 (-0.01, -0.01)	**-1.10 (-1.79, -0.42)**	100%	0.12 (-0.19, 0.47)	24%
7	Shuswap	1.69 (1.09, 2.41)	-0.02 (-0.03, -0.01)	-0.23 (-0.69, 0.18)	87%	0.00 (-0.25, 0.21)	47%
8	Chilliwack	4.27 (2.78, 5.75)	-0.04 (-0.06, -0.01)	**-1.32 (-2.59, -0.15)**	99%	-0.13 (-0.59, 0.22)	73%
9	Skokomish	1.74 (0.91, 2.58)	-0.74 (-1.00, -0.47)	**-1.14 (-2.03, -0.25)**	99%	0.17 (-0.02, 0.37)	4%
10	Skagit	2.49 (1.15, 3.87)	-0.09 (-0.11, -0.06)	-0.73 (-1.82, 0.37)	91%	-0.04 (-0.23, 0.14)	66%
11	Snohomish	2.62 (1.31, 3.91)	-0.16 (-0.23, -0.10)	**-1.64 (-2.71, -0.64)**	100%	0.03 (-0.17, 0.24)	36%
12	Stillaguamish	2.22 (0.79, 3.75)	-1.20 (-1.67, -0.84)	**-1.54 (-2.75, -0.45)**	100%	**0.22 (0.01, 0.42)**	2%
13	Green	2.43 (1.41, 3.35)	-0.13 (-0.19, -0.09)	**-1.75 (-2.83, -0.74)**	100%	0.00 (-0.19, 0.19)	53%
14	Lake Washington	3.08 (2.11, 4.02)	-0.98 (-1.31, -0.65)	**-1.82 (-2.70, -0.92)**	100%	-0.11 (-0.29, 0.07)	88%
15	Nisqually	3.10 (1.44, 4.91)	-1.15 (-1.57, -0.73)	-0.71 (-1.95, 0.57)	87%	-0.12 (-0.45, 0.17)	77%
16	Hoko	0.91 (-0.07, 1.99)	-1.24 (-1.62, -0.86)	0.01 (-0.59, 0.47)	45%	0.11 (-0.07, 0.29)	11%
17	Elwha	2.67 (0.12, 5.27)	-1.14 (-1.96, -0.32)	-0.85 (-2.18, 0.41)	91%	0.09 (-0.28, 0.52)	33%
18	Queets	2.91 (2.44, 3.37)	-0.12 (-0.19, -0.06)	**-0.53 (-0.71, -0.35)**	100%	-0.16 (-0.44, 0.09)	89%
19	Quillayute	3.28 (2.58, 3.95)	-0.12 (-0.17, -0.07)	**-0.66 (-0.91, -0.39)**	100%	-0.02 (-0.29, 0.24)	56%
20	Hoh	2.82 (2.34, 3.33)	-0.30 (-0.42, -0.19)	**-0.45 (-0.63, -0.26)**	100%	0.07 (-0.17, 0.31)	29%

For the Chinook salmon populations examined here, observed harvest rates dropped by an average of 45% over the range of brood years for which we had data. The Shuswap River was the only population where harvest rate increased (33%). However, our simulations suggest observed harvest rates still exceeded U_{MSY} in recent years for many populations, such as the Cowichan, Puntledge and Shuswap in the Strait of Georgia, the Skagit and Green in the Puget Sound, and all three populations on the Washington Coast (Queets, Quillayute, and Hoh).

2.4.7 Trends in wild Chinook salmon productivity

For many of the Chinook salmon populations we considered, our models suggest productivity declined between the late 1970s and early 1980s, and the mid-1990s (Fig. 2.7). Populations in east Vancouver Island (Cowichan, Quinsam, Qualicum), central Puget Sound (Snohomish, Stillaguamish, Green, Lake Washington), and Washington Coast (Queets, Quillayute, Hoh) showed the most pronounced drops in productivity, while Fraser River stocks (with the exception of the Chilliwack) were relatively stable. The two Juan de Fuca Chinook salmon stocks did not show any clear temporal patterns in productivity, nor did several stocks from the northern and southern regions on Puget Sound (Skagit, Skokomish, and Nisqually). Stocks that experienced the most pronounced drops in productivity between the 1970s and 1990s appear to be associated with negative q_i values whose posterior distribution did not overlap with zero (i.e., is “significant”) (Table 2.4). Following the declines in productivity that occurred between the 1970s and 1980s, many stocks exhibited somewhat stable trends after 1995. This appears to coincide with seal populations in the Salish Sea reaching carrying capacity (Olesiuk 2010) (Fig. 2.2). The best examples of this pattern are the Cowichan, Qualicum, and Chilliwack populations from the Strait of Georgia, the Stillaguamish and Green in the Puget Sound, and all three populations on the Washington Coast (Fig. 2.7).

2.5 Discussion

We evaluated the relationship between two biotic covariates (seal density and hatchery abundance) and productivity in 20 populations of wild fall Chinook salmon in British Columbia and Washington State and found negative relationships between Chinook salmon productivity and harbour seal density in 19 of the 20 populations, of which 14 were considered ‘significant’. Our model projections showed that increases in the number of harbour seals since 1970 was associated with an average decrease in MSY of 74%. Thus, predator density is associated with reduced productivity and yield in populations in most of the major Chinook salmon-producing rivers in lower-British Columbia and Washington State. In contrast, effects of hatchery abundance on wild stock productivity were mixed and weak in most populations, except for one population (Stillaguamish River) in central Puget Sound.

There is a tendency in analyses of fish recruitment to over-estimate the strength of correlations and predictive power (Shepherd et al. 1984; Myers 1998). Therefore, evaluating correlative evidence for causality in the absence of manipulative experiments requires consideration of such factors as 1) the strength of the correlation; 2) its consistency across multiple populations or units of observation; 3) mechanistic explanations from experiments, and 4) alternative/competing explanations (Hilborn 2016).

2.5.1 Effects of seal predation

The density of harbour seals in the Strait of Georgia, Puget Sound, and along the Washington coast was negatively associated with Chinook salmon productivity in nearly every population in these three regions. Scientists have been cognizant of the concurrent decrease in Chinook salmon abundance and the increase in seal numbers in the Salish Sea for at least two decades. However, the magnitude of decline in marine survival in Chinook salmon has not been consistent among the different populations (PSC 2015a, b; Ruff et al. 2017).

Our study is the first to assess the relationship between seals and Chinook salmon abundances at the population (sub-basin) scale in the Pacific Northwest. In addition, our approach provides a rigorous statistical framework to quantify the effect of biotic covariates on key management parameters.

Our model predictions are consistent with recent mechanistic evidence for a causal relationship between seal predation and declines in Chinook salmon marine survival since the 1970s. Most notably, new methods for quantifying juvenile salmon in predator diets have found seals targeting juvenile Chinook salmon more than chum (*O. keta*) and pink salmon (*O. gorbuscha*) smolts, despite the latter two species being much higher in abundance (Thomas et al. 2017). These studies show that the overall contribution to the seal diet is small during the spring and summer (typically < 5%), but potentially results in the loss of tens of millions of Chinook salmon smolts each year because of the large number of seals in the Strait of Georgia. Bioenergetics modeling further suggests that predation on Chinook salmon smolts by seals in the Puget Sound has probably increased 7-fold following enactment of the Marine Mammal Protection Act, and that as many as one in four hatchery smolts are eaten by harbour seals in recent years (Chasco et al. 2017a).

While much of the recent research involving seal predation in the eastern-Pacific has focused on the Salish Sea, including a major transboundary research effort (Riddell et al. 2009), our results suggest that seal predation on Chinook salmon from coastal stocks may also be of concern. The three coastal populations assessed showed very high probabilities of a significant negative relationship between seal densities and productivity (Fig. 2.5; Table 2.4). Additionally, populations along the Washington coast also appear to have experienced declines in productivity since the 1970s, although they appear to have stabilized at higher levels compared to those in the Strait of Georgia and Puget Sound (Fig. 2.3). It is possible that the relatively pristine freshwater and estuarine habitat of these coastal watersheds has buffered population productivity and abundance against factors causing poor marine survival, which may allow these populations to be harvested at higher rates than those from the Salish Sea (Fig. 2.7). Despite these modest harvest rates, our analysis suggests MSY for the Washington State's coastal populations has still been drastically reduced since 1970 (Fig. 2.5). Unfortunately, we were not able to investigate trends along the outer British Columbia coast (west Vancouver Island) due to the paucity of abundance data for harbour seals in this region (Olesiuk 2010).

2.5.2 Spatial patterns in predation

The strength and consistency of the correlations we detected may not be surprising given the clear inverse relationship between seals and salmon (Fig. 2.2). However, the weak degree of spatial relatedness of seal effects (q_i) among populations is noteworthy. One explanation for the weak spatial relatedness may be that there simply is not enough information in the data to detect a spatial (statistical) effect (Banerjee et al. 2015). Alternatively, it is conceivable that estuary location, which defines the "neighborhood" of our spatially-structured candidate models, was unimportant to, or was a poor proxy for, factors that determine the dynamics of seal predation during the first year that salmon are at sea.

The hypothesis that seal predation is highest for juvenile Chinook salmon outside the estuary is consistent with a recent study in the Strait of Georgia (Allegue et al. 2020). Harbour seals did not respond numerically or change their foraging behavior to target hatchery released Chinook salmon smolts during spring at the mouth of the Big Qualicum River on Vancouver

Island. It appears instead that some seals target the Chinook salmon smolts later in mid-summer when the fish are bigger (Allegue et al. 2020), which coincides with movement out of the estuaries to nearshore or offshore habitats (Healey 1980b; Duffy and Beauchamp 2011; Beamish et al. 2012). This may explain the high proportion of juvenile Chinook salmon found in the summer seal diet at a number of non-estuary sites (Lance et al. 2012; Thomas et al. 2017).

Table 2.5: Percent change in maximum sustainable yield (MSY) and harvest rate at MSY (U_{MSY}) between 1970 and the last year in the time series due to changes in each variable (seal density and hatchery abundance), for all 20 populations of Chinook salmon. Regions include the Strait of Georgia (SOG); Puget Sound (PS); Strait of Juan de Fuca (JDF), and Washington Coast (WA Coast).

			% Change in MSY		% Change in U_{MSY}	
Stock	**Stock Name**	**Region**	**Seal Density**	**Hatchery Releases**	**Seal Density**	**Hatchery Releases**
1	Cowichan	SOG	-94	44	-61	14
2	Puntledge	SOG	-51	12	-24	4
3	Nanaimo	SOG	-86	-31	-41	-9
4	Quinsam	SOG	-81	-33	-38	-11
5	Qualicum	SOG	-64	-14	-29	-5
6	Harrison	SOG	-88	57	-55	19
7	Shuswap	SOG	-47	1	-22	0
8	Chilliwack	SOG	-86	-29	-40	-9
9	Skokomish	PS	-78	72	-47	26
10	Skagit	PS	-54	-9	-25	-3
11	Snohomish	PS	-84	9	-50	4
12	Stillaguamish	PS	-80	71	-45	23
13	Green	PS	-91	-1	-64	-1
14	Lake Washington	PS	-87	-24	-55	-11
15	Nisqually	PS	-48	-21	-20	-8
16	Hoko	JDF	2	71	1	26
17	Elwha	JDF	-87	33	-52	11
18	Queets	WA Coast	-96	-24	-74	-11
19	Quillayute	WA Coast	-97	-3	-73	-1
20	Hoh	WA Coast	-89	9	-56	3
		Mean (95% CI):	-74 (-85, -64)	9 (-6, 25)	-44 (-52, -35)	3 (-2, 9)

There is evidence that smolts using regions with low predator densities may fare better than others. For example, in the Strait of Georgia, steelhead smolts originating from the same watershed were twice as likely to survive if they passed through Malaspina Strait, compared to those that migrated west of Texada Island (Furey et al. 2015). Similarly, trawl surveys found high abundances of sub-yearling Chinook salmon from the South Thompson River, a population whose marine survival rates have actually increased over the last two decades (Beamish et al. 2010a; Neville et al. 2015), rearing along the British Columbia's inner coastline from Malaspina Strait to Howe Sound (Neville, unpublished data). In terms of seal abundance in this area, aerial surveys have found significantly lower seal numbers along the inner stretch of coastline than in most regions of the Strait of Georgia (Olesiuk 2010). All told, this suggests that predation by seals on multiple stocks mixing in common rearing and foraging areas may be high during the summer months. This could explain why location of saltwater entry and its distance to the open ocean may not be as influential as we initially hypothesized.

The lack of spatial correlation among the coefficients calculated and the findings from other studies, suggest that predation effects on Chinook salmon are strongest outside the estuary at an across-basin scale. Interestingly, this does not appear to be the case for other Pacific salmon species of high conservation concern. Recent research suggests that seal predation on steelhead smolts in the Puget Sound occurs very shortly after ocean entry, and that early marine survival is lower for those fish that have longer migration routes to the open ocean (Moore et al. 2010; Moore and Berejikian 2017). In the Strait of Georgia the Big Qualicum River estuary is a foraging “hotspot” for a portion of the local seal population that specializes in targeting out-migrating coho smolts at the river mouth (Allegue et al. 2020). Other evidence similarly suggests that seal predation on coho salmon smolts is highest within the first month of ocean entry (see: Chapter 3). The apparent disparity in peak seal predation mortality on coho and steelhead, and Chinook salmon smolts, may be a function of prey size. Chinook salmon smolts may be too small compared to coho and steelhead smolts at ocean-entry to be worthwhile targeting (Tollit et al. 1997; Allegue et al. 2020; Thomas et al. 2017).

2.5.3 Effects of hatchery releases

There is some evidence that hatchery smolt abundance may negatively impact marine survival of Chinook salmon in the eastern Pacific (Levin et al. 2001), but our analysis does not support this. A few of the Chinook salmon populations analyzed had moderately high probabilities of a strong negative correlation between productivity and hatchery abundance (Table 2.4), but the only statistically 'significant' relationship we found was positive (Table 2.4). One possible explanation for a positive relationship between productivity and hatchery abundance could be predator swamping, which has been observed in freshwater habitats (Furey et al. 2016).

Although our best performing model had an exchangeable hierarchical prior on h (hatchery effect), we could not completely rule out the second ranked model (ΔDIC=2), which had a spatially-structured CAR prior (Table 2.3). Parameter estimates for this model imply that the hatchery effects on Chinook salmon populations occurring within 23 km of each other are correlated with productivity. Only stock combinations from the central Puget Sound region fell within this threshold: Green-Lake Washington, Stillaguamish-Skagit, Snohomish-Stillaguamish, and Snohomish-Skagit. However, uncertainty around the degree of spatial relatedness of hatchery effects (ω_h) was high, and no obvious patterns existed in the individual estimates of the hatchery effects. It therefore remains unclear from our analyses how hatchery smolt abundance impacts wild populations, and whether those impacts occur at local or regional scales.

2.5.4 Model assumptions

The structure of our model (Eq. 2.5) makes several important assumptions that warrant discussion. Most relevant to our key findings is our assumption that the functional relationship between predator and prey is Type I ($q_i\ x\ Seal_{j,t}$), and not subject to constraints of handling time (Holling 1965). However, this is likely not an issue here, as Peterman and Gatto (1978) found most predators of salmon smolts are not being saturated, and operate on the low end of the functional response curve. This likely applies to interactions between harbour seals and salmon smolts, as all species of juvenile salmon rarely make up more than 10% of the diet of harbour seals at any time throughout the year (Thomas et al. 2017).

A second assumption in our model implies that important alternative prey species are relatively constant over the time series in the analysis. Given comparable abundance time series for key alternative prey species including herring, hake, or pollock (Lance et al. 2012; Steingass 2017), it is plausible that a multi-species relationship could be integrated into this model structure (Walters et al. 1986). However, mass-balance ecosystem models or models of intermediate complexity (Plagányi et al. 2014) are probably better suited for multi-species inference.

2.5.5 Conclusions

Our analysis suggests that harbour seal predation could be driving productivity of wild Chinook salmon populations, but the correlative nature of our study and the inherent possibility of detecting spurious relationships demand treating these findings with caution. The same could be said about the ability of our models to capture important fine-scale interactions between wild populations and hatchery smolts, especially if these interactions are linked to predation or mediated by abundances of other prey species. Deliberate manipulative experiments are necessary to address methodological issues with our modeling approach, but predator control of seals may not be a viable option for political and ethical reasons (Yodzis 2001). However, hatcheries present a clear opportunity to engineer controlled, replicated experiments, and would provide a unique environment to explore questions related to functional relationships between seals and smolts.

Combined with the mechanistic evidence found in the recent diet, and bioenergetics of harbour seals studies conducted in the Salish Sea, it may be reasonable to conclude that the relationships we detected between Chinook salmon productivity and seal densities are causal. However, in addition to the increase in marine mammal predators, the Salish Sea and adjacent regions have seen other major ecosystem changes since the 1970s. These include increases in certain contaminates, introduction or proliferation of pathogens, habitat degradation, and changing ocean conditions, which all have the potential to impair the health and behavior of Chinook salmon in the early marine stage of life (Noakes et al. 2000; Magnusson and Hilborn 2003; O'Neill and West 2009; Irvine and Fukuwaka 2011). Therefore, it is conceivable that a composite of factors make juvenile Chinook salmon more vulnerable to predation by efficient, opportunistic predators like harbour seals. None of the approaches applied to date have the ability to evaluate the possibility that seals are merely a proximate source of mortality instead of the ultimate source.

The predatory impacts of seals on commercially important salmon populations are not unique to salmonids in the eastern Pacific. In the Baltic Sea, changing environmental conditions and prey availability appear to have exacerbated predation on Atlantic salmon (*Salmo salar*) post-smolts by gray seals (*Halichoerus grypus*), which have also increased in abundance since the 1980s (Mäntyniemi et al. 2012; Friedland et al. 2017). As conflicts continue to arise from concurrent conservation efforts to recover both predator and prey populations, pressure will increase to develop science-based management strategies and policy tools for navigating these challenges (Marshall et al. 2015; Samhouri et al. 2017). In the interim, studies such as ours highlight the importance of including predator-prey interactions in forecasting and assessment methods, and the need to seriously consider well-designed experimental manipulations to test hypotheses about predator-prey interactions and their impact on fisheries.

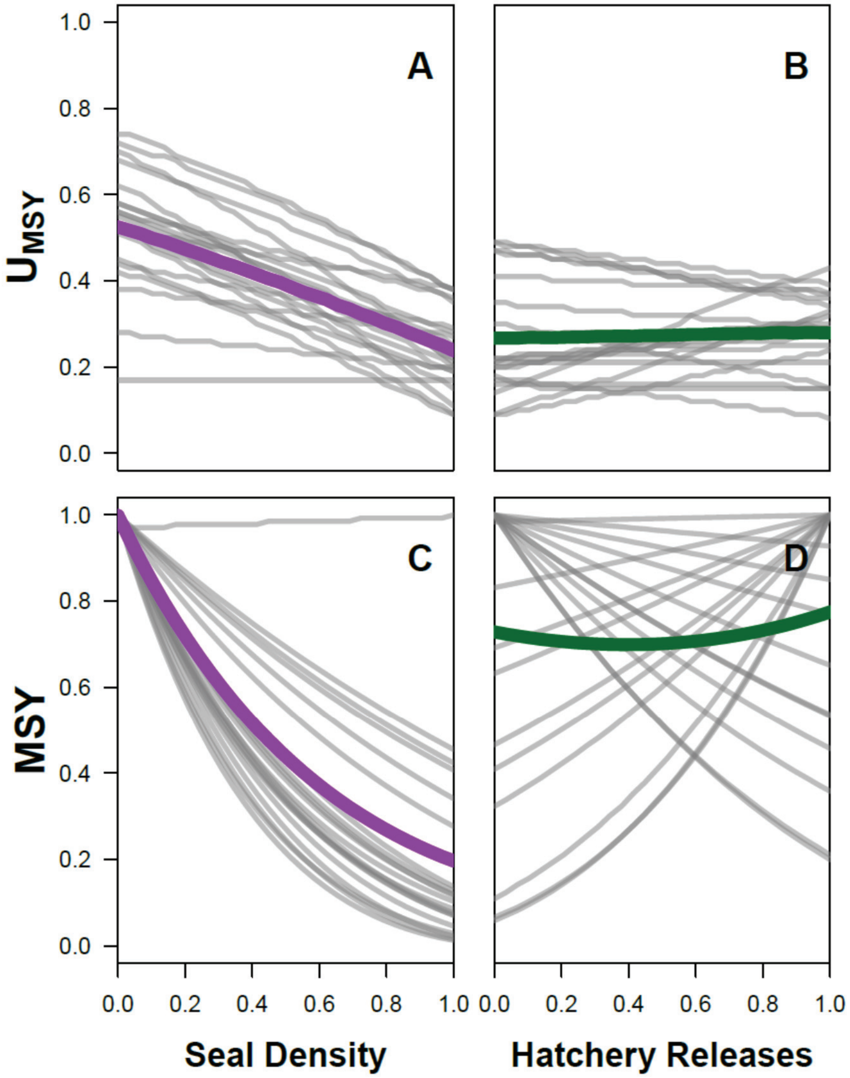

Figure 2.6: Plots show the harvest rate at maximum sustainable yield (U_{MSY}) and maximum sustainable yield (MSY) over a range of seal densities (A and C) and hatchery releases (B and D). The independent variable on x-axis is scaled from zero to the highest observed value (1.0) in the time series, while the other variable remains constant at the most recent value in the time series. MSY on the y-axis of plots C and D is scaled from zero to the largest value of MSY (1.0) for each stock. The grey lines represent the individual stocks, and dark lines show the mean U_{MSY} and MSY for all 20 stocks of Chinook salmon.

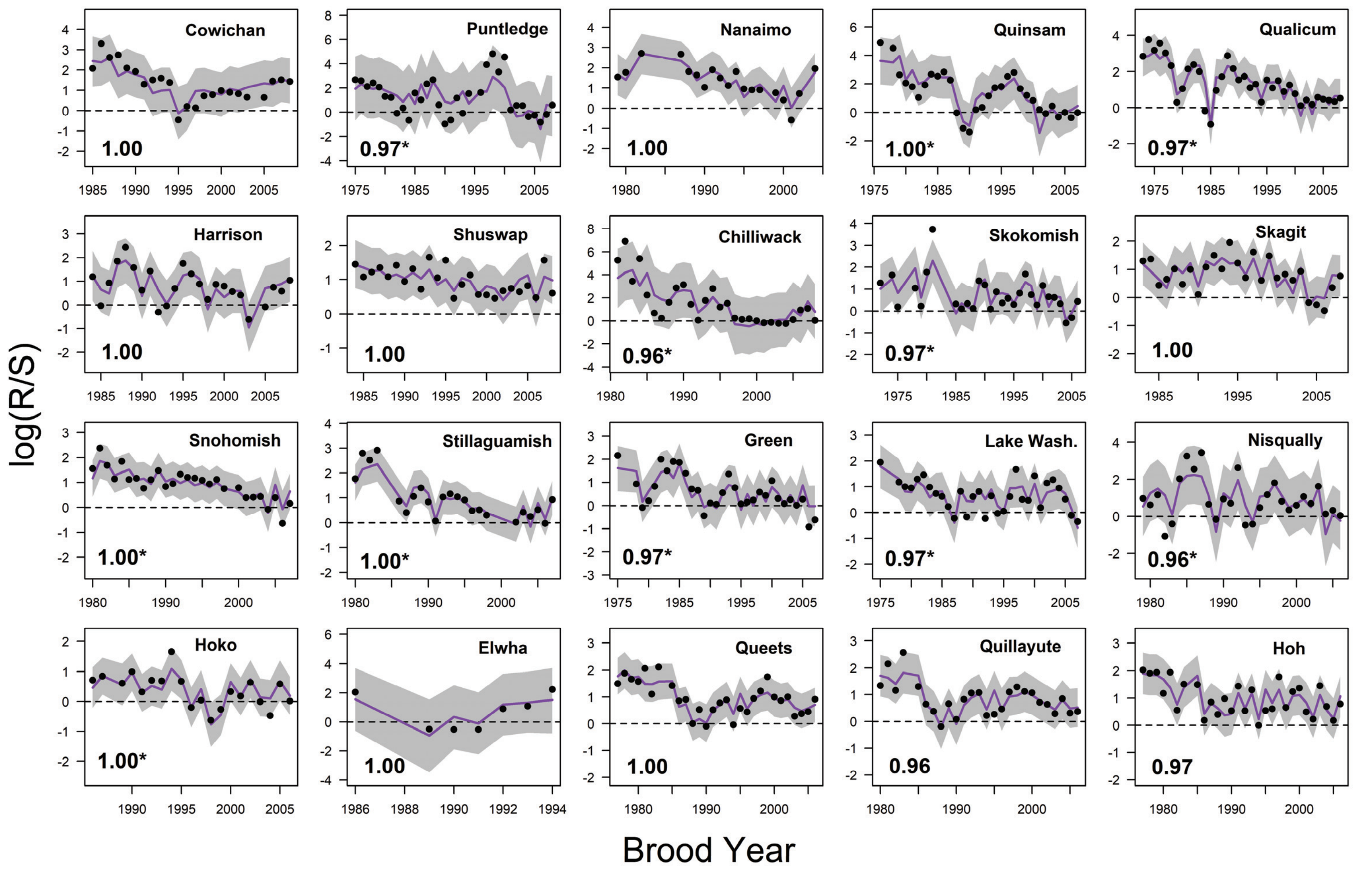

Figure 2.7: Log recruits per spawner of Chinook salmon by brood year, fit with Model 1. 95% posterior predictive intervals are depicted by the grey regions and posterior means are shown with solid lines. The data points (black circles) show the observed productivity calculated from the spawner-recruit data (Table 2.1). The proportion of the observed data points included in the predictive intervals are shown in the lower left region of each plot. Asterisks denote populations where autocorrelation among error residuals (ρ_i) was significant.

Chapter 3: Quantifying impacts of harbour seal predation on juvenile Chinook and coho salmon in the Strait of Georgia, British Columbia

3.1 Summary

The failure of Chinook and coho salmon populations in the Strait of Georgia to respond to reduced fishing pressure has led some to hypothesize that increases in harbour seal predation may be impeding recovery. However, it is not known how many juvenile Chinook and coho salmon they might consume. We estimated predation rates by combining diet data from 1,484 seal scats with a novel predation model that captures the prey demands of seals, and the growth, survival and abundance of juvenile Chinook and coho salmon. Our models suggest that the small proportion of juvenile salmon consumed by harbour seals (< 5% of the diet) constitutes a significant proportion of the annual production of juvenile Chinook and coho in the Strait of Georgia. We estimate that harbour seals consumed an annual average of 37-44% of juvenile Chinook salmon (13-14 million fish) and 46-59% of juvenile coho salmon (6-7 million), from 2004-2016. Our research suggests that harbour seal predation on young Chinook and coho salmon should be treated as a potentially important factor that affects productivity of salmon populations in the Salish Sea.

3.2 Introduction

Rapid increases in predator populations can alter ecosystem dynamics considerably, often posing serious challenges to natural resource managers tasked with achieving multiple conservation objectives (DeMaster et al. 2001; Marshall et al. 2015; Smith et al. 2015). Often, paucity of data can limit the ability to understand species interactions, and may thwart efforts to identify trade-offs or evaluate competing alternative management strategies. In many cases, abundance time-series are the only data available to establish relationships between predator and prey. While 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 strong correlation and a credible mechanistic explanation (Hilborn 2016), 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). While some stakeholders regard such recoveries as an unqualified conservation success story, the resulting ecological consequences of interactions between marine mammals and exploited or protected fish populations are often complex and unclear (Williams et al. 2011; Surma and Pitcher 2015).

Harbour 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) (Read and Wade 2000; Jeffries et al. 2003; Brown et al. 2005; Olesiuk 2010). In the early-1970s, harbour seals in the Strait of Georgia numbered less than 5,000 animals, while recent surveys suggest the population is between 35,000-40,000 animals (Olesiuk 2010; Majewski and Ellis, *in review*). In addition, surveys in Washington state suggest that harbour seals in the 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. Unsurprisingly, these trends in harbour seal abundances have prompted increased interest in the foraging ecology of these generalist predators (Olesiuk et al. 1990; Thomas et al. 2011; Howard et al. 2013), especially since abundances of valuable fish species like salmon and rockfish have declined severely over the same time period (Palsson et al. 2009).

Chinook (*Oncorhynchus tshawytscha*) and coho (*O. kisutch*) salmon populations in the Salish Sea experienced drastic declines in abundance and productivity in the l970s (Beamish et al. 2010a; Beamish et al. 2012; Preikshot et al. 2013). Researchers have investigated a number of plausible biotic and abiotic explanations: loss of freshwater and marine habitat (Nehlsen et al. 1991; Magnusson and Hilborn 2003); overfishing (Rutter 1997); hatchery practices (Irvine et al. 2013); interspecific competition (Ruggerone and Goetz 2004; Springer and van Vliet 2014); 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; Chasco et al. 2017a, b).

The failure of Chinook and coho salmon populations in the Salish Sea to respond to reduced fishing pressure has led some to hypothesize that increases in natural mortality on juvenile fish from upper trophic levels, such as pinnipeds, may be preventing the recovery of some salmon and steelhead (*O. mykiss*) populations (Beamish et al. 1997; Beamish et al. 2010a; Sobocinski et al. 2020). Pinnipeds are often suspected of inflicting significant damage to 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 harbour seals may consume a major portion of the number of juvenile Chinook and coho salmon residing in the Strait of Georgia, despite making up a minor portion of the overall harbour seal diet (usually less than 5%) (Thomas et al. 2017).

Previous attempts to estimate the number of Chinook eaten by seals in the Salish Sea (Chasco et al. 2017a, b) have raised concerns about model assumptions related to seal diet data that need to be addressed (Nelson et al., *in review*). Additionally, there has not yet been a similar effort to estimate the number of juvenile coho consumed annually by seals, despite a strong negative association between coho survival rates and seal abundance (Sobocinski et al., *in review*). Thus, improved estimates of juvenile Chinook and coho salmon lost to seal predation each year in the Strait of Georgia are important for identifying the most important factors affecting the productivity of both salmon species.

In this chapter, we estimated seal predation rates on juvenile Chinook and coho salmon by combining diet data from seal scats with a novel predation model that captures the prey demands of seals, and the growth, survival and abundance of juvenile salmon. We use this model not only to estimate current predation rates, but also to infer how natural mortality rates may have changed for both salmon species since the 1970s. Thus, we attempted to assess whether predation by harbour seals on young Chinook and coho salmon has negatively affected productivity of salmon populations in the Salish Sea.

3.3 Methods

3.3.1 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 United States in Washington State, and consists of three main sub-regions: the Strait of Georgia, the Puget Sound, and Strait of Juan de Fuca (Fig. 3.1). Its close proximity to two major metropolitan areas—Vancouver and Seattle—make it a vital component of both country's fishing industries; it serves as a fishing ground and a hub for fleets that target stocks throughout the north Pacific. The Salish Sea provides habitat for a multitude of commercially and recreationally important fish stocks, many of which have seen significant declines in catch and abundance since the mid-1980s (Harvey et al. 2012; Preikshot et al. 2013; Walters et al. 2020).

3.3.2 Predation model

We quantified the impact of seal predation on Chinook and 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 the 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 of the harbour 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 and Chinook salmon can be modelled 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 in 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 the marine environment (Parker 1968, 1971).

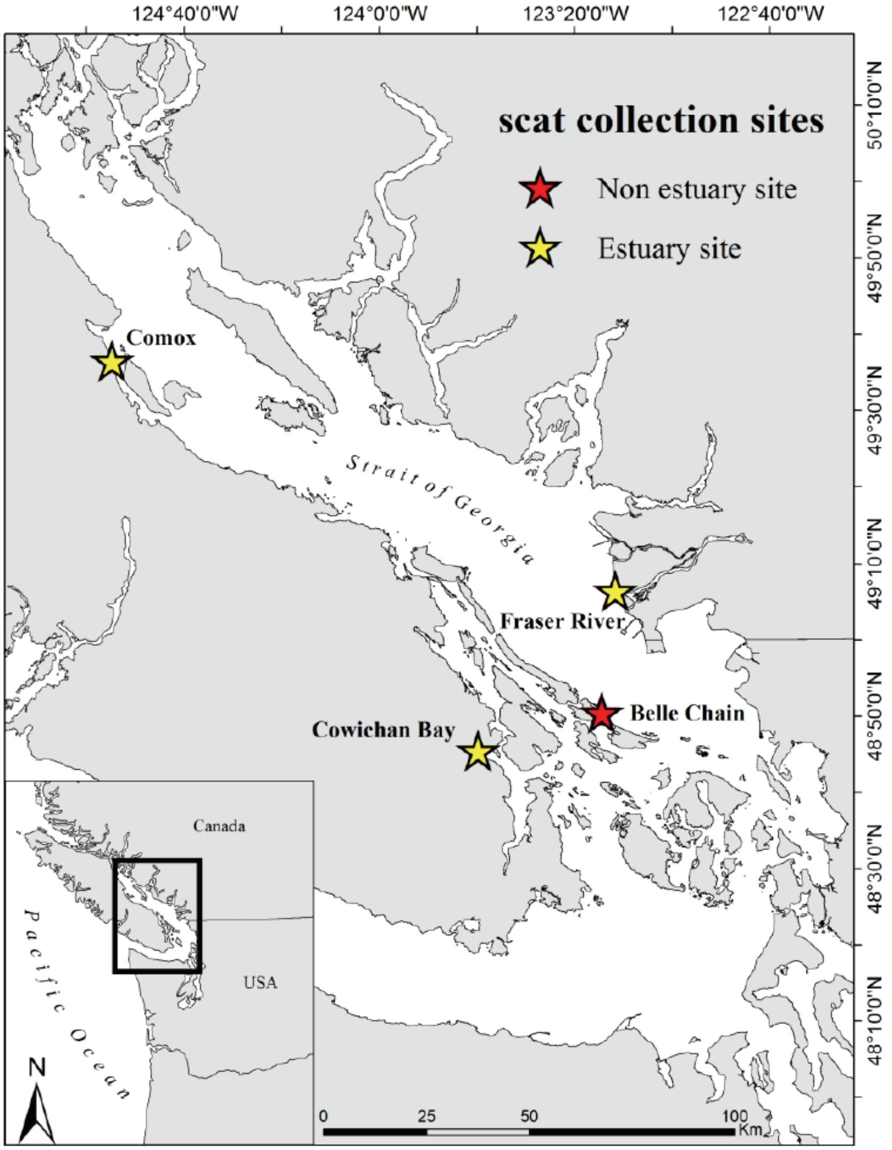

Figure 3.1: Locations of harbour seal haulouts in the Strait of Georgia, British Columbia, Canada, where scat collections occurred. The four sites include three estuary haulouts (Fraser River, Cowichan Bay, and Comox) and one non-estuary haulout (Belle Chain). See Table 3.2 for a summary of the exact locations and sample sizes for each site. (Map credit: A. Thomas)

3.3.2.1 Salmon abundance data

Calculating the mortality/predation rates of Chinook and coho salmon 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 Chinook and coho salmon that originate from streams and rivers within the Strait of Georgia (Fig. 3.1). While juvenile Chinook and coho salmon move among basins in the Salish Sea throughout the spring and summer (Rice et al. 2011; Beacham et al. 2016), the goal here was to estimate prey predation rates only for the Strait of Georgia.

Annual hatchery production for both species was calculated by collating publicly available release records from the RMIS database (www.rmpc.org; accessed June 1, 2019). In the Strait of Georgia basin, hatchery releases of Chinook salmon average between 12-15 million fish per year in recent years, while the number of hatchery-origin coho salmon released is typically between 5-10 million fish per year (Fig. 3.2; Table B3). 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). For Chinook and coho salmon, downstream/freshwater survival rates from release to saltwater are likely to vary considerably by watershed, and probably average between 50-90% (Bradford 1995; Quinn 2018). Based on recent estimates from tag experiments in the Cowichan River (Pellett, unpublished data), we assumed that the freshwater survival rates were 50% for Chinook salmon, and 70% for coho salmon (Melnychuk 2009). We estimated total juveniles entering the Strait of Georgia each year (y) as:

(Eq. 3.1)
$$N_{0_{s,y}} = \gamma_s N_{s,y}^{Natural} + \gamma_s N_{s,y}^{Hatchery}$$

where γ_s is the species-specific freshwater/downstream survival rate, and $N_{0_{s,y}}$ is the initial number of fish of species s 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.

Estimating ocean entry numbers of natural-origin Chinook and coho salmon was less straightforward than hatchery-origin salmon, as there are no public or private records of the hundreds of individual streams that produce juvenile Chinook and 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. While there is currently no comprehensive database or study of juvenile production from major Chinook salmon-producing rivers in the Strait of Georgia, annual escapement estimates are recorded by DFO-Pacific in the NuSEDS database (https://open.canada.ca/data/en/dataset). A previous study used this database to estimate a recent five-year average Chinook salmon escapement for the Strait of Georgia at approximately 461,000 spawners (Nelson et al. 2019a). We assumed a 1:1 female-to-male ratio of spawners, then used an estimate of 220 juveniles per female (Chasco et al. 2017b) to calculate the mean annual production. Assuming a 50% downstream/freshwater survival rate, this resulted in approximately 25.4 million Chinook smolts per year. For natural-origin coho salmon, we used an estimate of annual smolt production from an existing model that used 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.

3.3.2.2 Harbour seal abundance data

A time-series of harbour seal abundances in the Strait of Georgia is available from DFO's published aerial surveys in British Columbia (Olesiuk 2010). Actual count data are not available every year—typically every 2-3 years— so we used model-estimated abundances from the previous chapter, wherein a state-space model was fit to aerial survey data (see: Chapter 2 and/or Nelson et al. 2019b) (Fig. 3.2; Table B3).

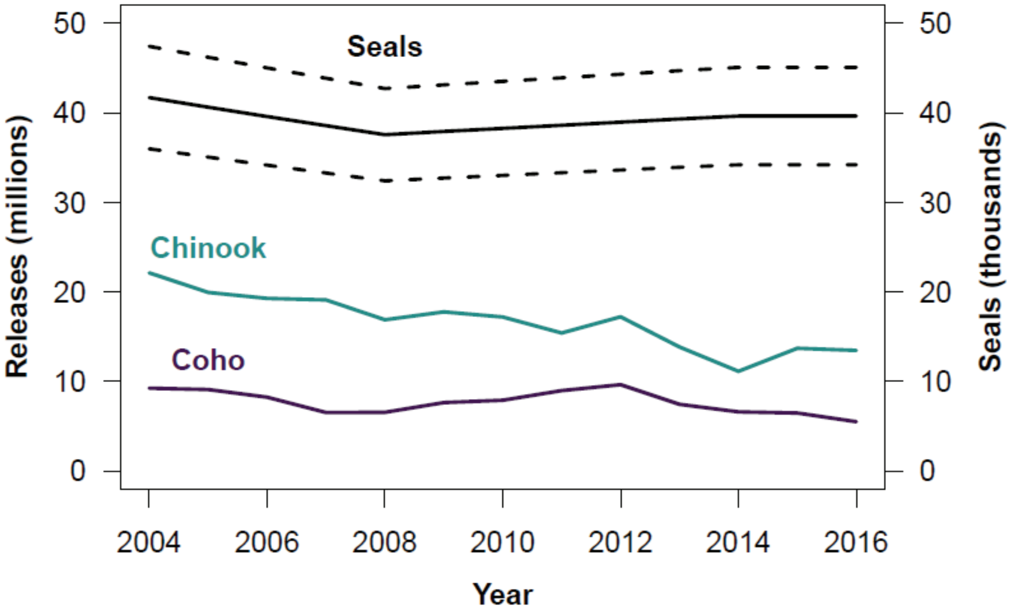

Figure 3.2: Annual harbour seal abundance (black), and hatchery releases of Chinook (teal) and coho (purple) salmon in the Strait of Georgia. Black dashed lines are the 95% confidence intervals around the estimates of seal abundance, assuming a coefficient of variation of 0.07 (Olesiuk 2010). Annual hatchery releases of Chinook and coho salmon were calculated from entries in the RMIS database (www.rmpc.org; accessed June 2019).

3.3.2.3 Harbour seal diet data

Harbour seal scat samples were collected from haul-outs at four different locations in the Strait of Georgia, British Columbia (Fig. 3.1; Table 3.2), between April and December, from 2012-2014. Scat collections were conducted by researchers from the University of British Columbia under Federal Permits MML 2011-10 and MML 2014-07 from the Department of Fisheries and Oceans, Canada, and under Animal Care Permit A11-0072, which was approved by the University of British Columbia. A detailed description of scat collection protocols is available in Thomas et al. (2017) and Voelker et al. (2020). Essentially, this dataset consists of the samples from Thomas et al.'s (2017) previous study, in addition to 288 samples collected in Cowichan Bay between April-December of 2014 (Fig. 3.1; Table 3.2).

We combined the diagnostic hard structures (e.g., otoliths, bones) with DNA extracted from each scat sample to estimate the proportion of salmonids (by species) in the seal diet using Thomas et al.'s (2017) DNA metabarcoding approach. 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 the presence/absence and/or co-occurrence of juvenile and adult hard parts with DNA, and on known seasonal life-history information. We used the resulting diet sample proportions to calculate monthly averages for each prey species, 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 3.3).

3.3.2.4 Predation model formulation

In each year y, an initial cohort of out-migrating smolts of species s leaving freshwater in the spring ($N_{0_{s,y}}$) is subjected to a total natural mortality rate, which is the sum of mortality from harbour seal predation and all other sources. 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,…,T; T=52):

$$N_{s,t+1,y} = N_{s,t,y} exp\left[\left(-M_{s,t}^{Other} - M_{s,t,y}^{Seal}\right)t\right] \quad \text{(Eq. 3.2)}$$

Table 3.1: Symbols, descriptions, values, and sources/references for parameters, variables and indices in the harbour seal predation model.

Symbol	Description	Value(s)	Source(s)
$\boldsymbol{S_y}$	Seal abundance	Appendix A; Normal (S_y, CV=0.07)	Olesiuk 2010; Nelson et al. 2019b
$\boldsymbol{Q}$	Seal daily energetic requirement (kg)	Uniform (1.9, 2.1)	Olesiuk 1993; Howard et al. 2013
$\boldsymbol{p_{s,t}}$	Monthly seal diet proportion	Table 3	Thomas et al. 2017; Nelson, unpublished data; Voelker et al. 2020
$\boldsymbol{\alpha}$	Allometric constant	9.61	Nelson et al. 2019a
$\boldsymbol{\beta}$	Allometric constant	3.07	Nelson et al. 2019a
$\boldsymbol{\gamma_s}$	Freshwater/downstream survival proportion	Coho: 0.70 Chinook: 0.50	Bradford 1995; Melnychuk 2009; Pellett, unpublished data
$\boldsymbol{M_s^{Ref}}$	Instantaneous mortality at reference length	Estimated	-
$\boldsymbol{c_s}$	Allometric mortality exponent	Estimated	Lorenzen 1996, 2000
$\boldsymbol{g}$	Monthly growth increment (cm)	Coho: 3.0 Chinook: 2.0	Argue et al. 1983
$\boldsymbol{l_{0_s}}$	Initial prey length (cm)	Coho: 10.0 Chinook: 8.0	Argue et al. 1983; Beamish et al. 2008; Beamish et al. 2011
$\boldsymbol{l_s^{Ref}}$	Reference length (cm)	Coho: 75 Chinook: 85	www.fishbase.org
$\boldsymbol{N_{0_{s,y}}}$	Initial prey abundance	Table B3	Korman and Tompkins, 2014; Nelson et al. 2019a; Chasco et al. 2017b; NuSEDS database
$\boldsymbol{\sigma_{s,y}}$	SD of trawl surveys	Coho: CV=0.30 Chinook: CV=0.21	Beamish et al. 2010b, 2012
$\boldsymbol{s}$	Prey species	Coho, Chinook	-
$\boldsymbol{t}$	Week	t=1…T; T=52	-
$\boldsymbol{y}$	Year	2004:2016	-

Non-seal mortality $M_{s,t}^{Other}$ is a function predicted from a "reference" mortality rate at the species' asymptotic length relative to their current size (see: Lorenzen 1996, 2000):

(Eq. 3.3)
$$M_{s,t}^{Other} = \frac{M_s^{Ref}\left(\frac{l_s^{Ref}}{l_{s,t}}\right)^{c_s}}{T}$$

where M_s^{Ref} is the instantaneous natural mortality rate at the reference length l_s^{Ref}; $l_{s,t}$ is the length in week t, which is the length from the previous week plus a weekly growth increment ($l_{s,t+1} = l_{s,t} + \frac{g_s}{4.35}$) that is constant (Argue et al. 1983; Fisher and Pearcy 1995)—weekly growth is simply the monthly growth increment g_s partitioned into weekly intervals. c_s is the allometric length exponent that shapes the function (c=1.0 implies a mortality rate inversely proportional to length).

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

(Eq. 3.4)
$$M_{s,t,y}^{Seal} = \left(\frac{E_{s,t,y}}{N_{s,t,y}}\right)\frac{\left(M_{s,t,y}^{Other} + \frac{E_{s,t,y}}{N_{s,t,y}}\right)}{1 - exp\left[-\left(M_{s,t,y}^{Other} + \frac{E_{s,t,y}}{N_{s,t,y}}\right)\right]}$$

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

(Eq. 3.5)
$$E_{s,t,y} = \frac{p_{s,t}V_y}{w_{s,t}}$$

where $p_{s,t}$ is the mean proportion of salmon in the seal diet in week t, and V_y is the weekly biomass of all prey consumed by the seal population. Note that Eq. 3.4 is overly complex for weekly calculations over which change in N_s is relatively small; the same basic result can be obtained simply by setting the weekly $M_{s,t}^{Seal} = \frac{E_{s,t}}{N_{s,t}}$. The length-to-weight conversion for prey is an exponential relationship commonly used for salmonids (Froese 2006) (Fig. B1-B2):

(Eq. 3.6)
$$w_{s,t} = \frac{\alpha\left(l_{s,t}\right)^{\beta}}{1 \times 10^5}$$

where $l_{s,t}$ is the mean length in week t, and α and β are allometric parameters for juvenile salmonids (Table 3.1), which were estimated using length/weight data from a previous study (Nelson et al. 2019a). The weekly total biomass of prey consumed for the seal population is estimated as the product of the seal population abundance (S_y) times the average daily prey requirement, by mass (Q) in kg:

(Eq. 3.7)
$$V_y = \left(S_y Q\right) \times 7$$

We assumed the average harbour seal in the Strait of Georgia requires between 1.9-2.0 kg of prey per day (Table 3.1), which is based on the mean estimated daily requirements from the two most comprehensive bioenergetics studies of harbour seals in the Salish Sea (Howard et al. 2013; Olesiuk 1993). These and other studies suggest harbour seals consume a diverse diet typical of a generalist predator, but proportions of their major dietary components like clupeids (Pacific herring), gadoids (Pacific hake [*Merluccius productus*], walleye pollock [*Gadus chalcogrammus*]) and adult salmon appear to be relatively consistent in the Salish Sea (Olesiuk et al. 1990, Lance et al. 2012, Howard et al. 2013). 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 use diet data from different regions (Strait of Georgia vs. Puget Sound) and decades (1980s vs. 2000s)—suggests variability is probably low when generalizing the daily prey requirements over entire population.

3.3.2.5 Model fitting

To estimate the mortality rates, numbers of individual fish consumed by harbour seals, and other quantities of interest, we used several parameter values available in the literature (Table 3.1). While some parameters used in the model are well-established from recent empirical studies (e.g., harbour seal abundance, daily energetic requirement), others are uncertain, or are not well studied. In particular, the allometric length exponent (c_s), and the instantaneous mortality rate at each species' reference length (M_s^{Ref}) are difficult to estimate from the information available in the literature. The allometric length exponent is likely very close to 1.0 for both coho and Chinook salmon, but the only estimates for the genus are for rainbow trout (*O. mykiss*) in captive (i.e., hatchery) studies (Lorenzen 2000). M_s^{Ref} at the reference length (l_s^{Ref}) used in this study corresponds with the mortality rate of sub-adult coho and Chinook 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, killer whales). 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 these poorly-known parameters (M_s^{Ref} and c_s), by fitting our predation models to 13 estimates (for each species) of juvenile salmon abundance in the month of September, which are estimated from trawl surveys in the Strait of Georgia (Beamish et al. 2010b; Boldt et al. 2019). We assumed deviations between the natural logs of the observed and model-predicted abundances to be normally distributed, and used the following objective function to fit the models:

(Eq. 3.8)

$$L_s = \prod_{y=2004}^{2016} \frac{1}{N_{s,Sept,y}^{Obs}\sqrt{2\pi\sigma_s^2}} exp\left[\frac{\left(ln\left(N_{s,Sept,y}^{Obs}\right) - ln\left(N_{s,Sept,y}\right)\right)^2}{2\sigma_s^2}\right]$$

where $\sigma_s^2 = ln(CV_s^2 + 1)$ is the variance on the log scale, $N_{s,Sept,y}^{Obs}$ is the observed abundance, and $N_{s,Sept,y}$ is the model-predicted abundance. We assumed the CV of the trawl surveys for juvenile coho salmon to be 0.30, which was the mean of four published surveys conducted between 2004-2007 (Beamish et al. 2010a). For Chinook abundance via trawl surveys, we assumed a CV of 0.21 (Beamish et al. 2012). Function minimization—in addition to all other quantitative analysis—was performed in R (R Core Team. 2017), and the negative log-likelihood $-ln(L_s)$ was minimized using the "optim" function with the "BFGS" algorithm.

Table 3.2: Summary of harbour seal scat collection data from four sites in the Strait of Georgia. For each collection site (locations shown in Fig. 3.1), the location, total sample size, collection years and collection months are shown, in addition to the source of the data.

Site	Lat./Long.	Sample size	Collection years	Collection months	Source
Cowichan Bay	48°44'14.28"N, 123°37'17.76"W	595	2012-2014	April-December	Thomas et al. 2017; Voelker et al. 2020
Comox	49°35'45.53"N, 124°52'4.39"W	395	2012-2013	April-November	Thomas et al. 2017
Fraser Delta	49° 4'27.17"N, 123° 8'49.46"W	311	2012-2013	April-October	Thomas et al. 2017
Belle Chain	48°58'10.73"N, 123°29'34.63"W	183	2012-2013	April-October	Thomas et al. 2017

Table 3.3: Monthly mean diet proportions of juvenile Chinook and coho salmon in the harbour seal diet. Diet proportions are based on 1,484 scat samples from four haul-out sites, collected between April and December from 2012-2014.

Month	Sample size	Chinook	Coho
April	74	0.012	0.048*
May	158	0.015	0.005
June	152	0.031	0.026
July	178	0.038	0.038
August	189	0.014	0.009
September	336	0.014	0.001
October	303	0.005	0.006
November	83	0.000	0.000
December	11	0.000	0.000

*** Diet proportions for coho in the first three weeks of April are set to zero, as out-migrating coho salmon likely do not reach the ocean until late-April, at the earliest.**

3.3.3 Predation model validation

While the predation model described above provides a relatively simple 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_s^{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_s^{Summer}, the period of high seal predation and a component of total mortality during the first year at sea M_s^{Total}. With these equations, we used a basic Monte Carlo simulation to generate a broad “prior” estimate of seal predation for each prey species that does not depend on estimating a base mortality rate like the one in the predation model. This can be used as a way to validate the previous method without assuming complete additivity of the mortality components. The approach also allowed us to depict uncertainty in parameters where there is a lack of data and/or precision (e.g., freshwater survival) (Table B1).

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

(Eq. 3.9) $$M_s^{Total} = M_s^{Fresh} + M_s^{Summer} + M_s^{Winter}$$

where M_s^{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_s^{Summer} is mortality rate during the summer months (e.g., May-September) when seal predation occurs, and M_s^{Winter} is mortality rate occurring from the fall until the end of the first ocean year of life the following calendar year. M_s^{Summer}can be partitioned into two components:

(Eq. 3.10) $$M_s^{Summer} = M_s^{Seal} + M_s^{Other}$$

where $M_s^{Seal}$is the seal predation component, and $M_s^{Other}$is a simultaneous ongoing, and potentially high, summer mortality rate due to factors other than seal predation. By varying the M_s^{Seal} and M_s^{Other} components of Eq. 3.10, we generate alternative hypotheses about the additive importance of seal-related mortality M_s^{Seal} while maintaining a total M_s^{Summer} estimate that is consistent with the juvenile trawl survey data.

For coho salmon, scattered observations of freshwater/downstream mortality rates from release to ocean entry indicate a substantial loss, with M_s^{Fresh} as high as 0.69 (Bradford 1995;

Melnychuk 2009). For Chinook salmon, recent tagging studies on the Cowichan River on east Vancouver Island suggest even higher mortality rates, perhaps as high as 1.0 (Pellett, unpublished data). For both species, the over-winter mortality rate M_S^{Winter} is likely much lower, probably not exceeding 0.60 (Argue et al. 1983). After the first year of life, the [recent] estimates of total instantaneous mortality for Chinook salmon range between 4.0-5.0 year^{-1} (Kendall et al. 2020), while rates for coho salmon are probably between 3.0-4.0 year^{-1}, on average (Zimmerman et al., 2015).

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

(Eq. 3.11) $$M_S^{Summer} = M_S^{Total} - M_S^{Fresh} - M_S^{Winter}$$

For the summer period when M_S^{Seal} and M_S^{Other} are occurring simultaneously, we used a Baranov-type catch equation, similar to the one in the previous section (Eq. 3.4), to predict the net number of fish killed E_S' by each of the mortality agents. In particular, the Baranov prediction of seal E_S' is given by

(Eq. 3.12) $$E_S' = \left(\frac{M_S^{Seal}}{M_S^{Summer}}\right) N_S e^{\left(-M_S^{Fresh}\right)} \left[1 - e^{\left(-M_S^{Summer}\right)}\right]$$

where N_S is the number of smolts at the start of the stanza; this equation simply partitions the total number of summer deaths over that stanza (number surviving to enter the summer ocean period times the proportion dying in the period given by $[1 - Survival_S^{Summer}]$). For a given consumption estimate E_S' and set of M_S^{Fresh}, M_S^{Winter} values, we can solve this equation for the seal predation rate M_S^{Seal}, as

(Eq. 3.13)
$$M_s^{Seal} = \frac{E_s'}{N_s e^{\left(-M_s^{Fresh}\right)}} \times \frac{M_s^{Summer}}{1 - e^{\left(-M_s^{Summer}\right)}}$$

and then calculate M_s^{Other} by subtraction: $M_s^{Other} = M_s^{Summer} - M_s^{Seal}$. Note that an indication of nonsensical values in Eq. 3.13 is given by negative estimates of M_s^{Other}. Varying the E_s' value in Eq. 3.13 leads to alternative hypotheses about the additivity of mortality caused by the estimated consumption by predators.

The set of equations described above were applied in a Monte Carlo simulation (10,000 draws) using the range of parameter values summarized in Table B1 to generate a prior distribution for seal-related mortality during the summer M_s^{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.

3.4 Results

3.4.1 Harbour seal diet

A total of 1,484 scat samples were collected from all four sites between April-December, during the years 2012-2014 (Tables 3.2-3.3). The highest monthly sample size occurred in September (n=336), while December was the month during which the fewest number of samples (n=11) were collected. Samples from Cowichan Bay (n=595) made up the largest percentage (40.1%) of the dataset, while the Belle Chain islets produced the fewest (n=183; 12.3%). Juvenile Chinook and coho salmon were present in the harbour seal diet from April through October; neither species occurred in the diet (as juveniles) during November or December (Table 3.3). Interestingly, the largest mean monthly diet percentage for both species was 3.8% during the month of July (Table 3.3). A more detailed analysis of this dataset (excluding 288 samples collected from Cowichan Bay in 2014) can be found in Thomas et al. (2017). This study includes seal diet proportions of other species of Pacific salmon, in addition to Chinook and coho salmon, in addition to an assessment of the spatial and temporal aspects of the data.

3.4.2 Parameter estimation and model fit

Initial fits of the predation models revealed strong confounding between the M_s^{Ref} and c_s parameters for both prey species. Thus, we elected to fix c_s and keep M_s^{Ref} as a free parameter in the estimation. Given that previous studies suggest c_s is close to 1.0 for Pacific salmonids (Lorenzen 2000), we chose this value as the "base case" scenario, then evaluated four alternative models (for each species) that assumed c_s was larger or smaller than 1.0 by 10% and 20%. We compared the alternative models with the base case using small-sample Akaike Information Criteria (AICc), which suggested no meaningful differences for either species (< 2 AICc unit difference) (Table B2). Accordingly, we proceeded to use the predation models for both Chinook and coho salmon with c_s fixed at 1.0. The predation models fit the observed abundance data from trawl surveys reasonably well for both Chinook and coho salmon (Figs. 3.3 and 3.4; Tables 3.4 and 3.5). For both Chinook and coho salmon, the mean observed September abundance fell within the 95% probability interval of the model-predicted abundance in 12 of the 14 years of data (Figs. 3.3-3.4). Estimates for M_s^{Ref} for the Chinook and coho salmon predation models were 0.39 year^{-1} (SE: 0.05) and 0.47 year^{-1} (SE: 0.09), respectively. These estimates translate to survival rates at reference length (l^{Ref}) of 68% for Chinook salmon, and 63% for coho salmon.

3.4.3 Predation rates on juvenile salmon

The median estimated number of juvenile Chinook salmon consumed by harbour seals in the first year at sea (April-March) ranged from 12.7-14.1 million individuals per year during

2004-2016 (Table 3.4). This equates to median estimates of proportions of the annual cohort of Chinook salmon lost to seal predation ranging from 0.37-0.44 (Fig. 3.3; Table 3.4). These estimates suggest that, during the marine phase, seal predation accounts for between 39-47% of natural mortality during the first year. For coho salmon, our model estimated median annual losses to seal predation of between 6.4-7.0 million juveniles (Fig. 3.4; Table 3.5). Thus, the median estimates of the annual proportion of the cohort lost to seal predation ranged from 0.46-0.59. This equates to median estimates of 44-59% of total natural mortality from seal predation during the first year at sea. If we assume freshwater productivity did not change significantly between 1970-2016 for either species, total annual instantaneous mortality from harbour seal predation during the first year at sea increased from 0.08 year^{-1} (95% CI: 0.05-0.11) to 1.47 year^{-1} (95% CI: 0.81-8.01) on Chinook salmon, and from 0.10 year^{-1} (95% CI: 0.08-0.13) to 1.78 year^{-1} (95% CI: 1.05-8.00) on coho salmon (Fig. 3.7; Table 3.5). In 1970, seals consumed an estimated 4.0% (95% CI: 3.4-4.6%) of juvenile Chinook salmon and 6.7% (95% CI: 5.8-7.7%) of coho salmon (Fig. 3.7). By 2016, our model estimates that those percentages had risen to 41.8% (95% CI: 35.4-48.1%) if Chinook salmon, and 59.4 (95% CI: 50.7-68.5%) of coho salmon (Fig. 3.7).

For Chinook salmon, our model estimates imply that non-seal mortality exceeded seal-related mortality shortly after the out-migration period between April and early-May (Fig. 3.5). After the first 1-2 months at sea, mortality from seal predation increased steadily to eventually exceed other sources of natural mortality between June and late-summer/early-fall (Fig. 3.5). In all years, the median weekly mortality rate from seal predation peaked in the summer, between June-August. For juvenile coho salmon, median peak mortality from seal predation occurred from ocean entry in late-April until early-May (Fig. 3.6). A secondary peak in seal-related mortality also occurred in all years during the summer months between July-August, around the same time as peak seal mortality on Chinook salmon.

3.4.4 Predation model validation

All annual median estimates of M_s^{Seal} from the predation model fell between the 2.5% and 97.5% quantiles of the "prior" distribution for both prey species (Fig. 3.8). Using the values of E_s', and M_s^{Fresh} and M_s^{Winter} from Eq. 3.12 gives a median M_s^{Seal} estimate of 1.19 (95% CI: 0.73-1.83) for coho salmon, and 1.57 (95% CI: 1.06-2.34) for Chinook salmon. The median estimates of M_s^{Seal} are somewhat lower than the implicit estimates of around 2.0 obtained for both species from regressions of M_s^{Total} on seal abundance (Chapter 2 and Nelson et al. 2019b; Walters, unpublished data). Non-seal mortality rates ($M_s^{Fresh} + M_s^{Other} + M_s^{Winter}$) were 2.28 (1.67-2.92) for coho salmon, and 2.90 (2.18-3.56) for Chinook salmon, which were comparable to the observed survival/mortality rates observed in the late-1970s, when survival rates for coho salmon typically ranged between 10-15%, and around 5% for Chinook salmon (Zimmerman et al. 2015). The M_s^{Seal} estimates were of course sensitive to the estimates of seal consumption E_s', and are also very sensitive to assumed [initial] smolt numbers N_{0_s}. For coho salmon in particular, the estimated natural smolt abundances are likely biased upward due to incomplete sampling of CWT in the escapement (Korman and Tompkins 2014). Assuming a lower N_{0_s}, due to the CWT bias problem, results in higher estimates of seal predation rates M_s^{Seal}. Likewise, higher assumed values for freshwater mortality M_s^{Fresh}lead to higher M_s^{Seal} estimates, and higher estimates of M_s^{Winter} lead to lower estimates of M_s^{Seal}.

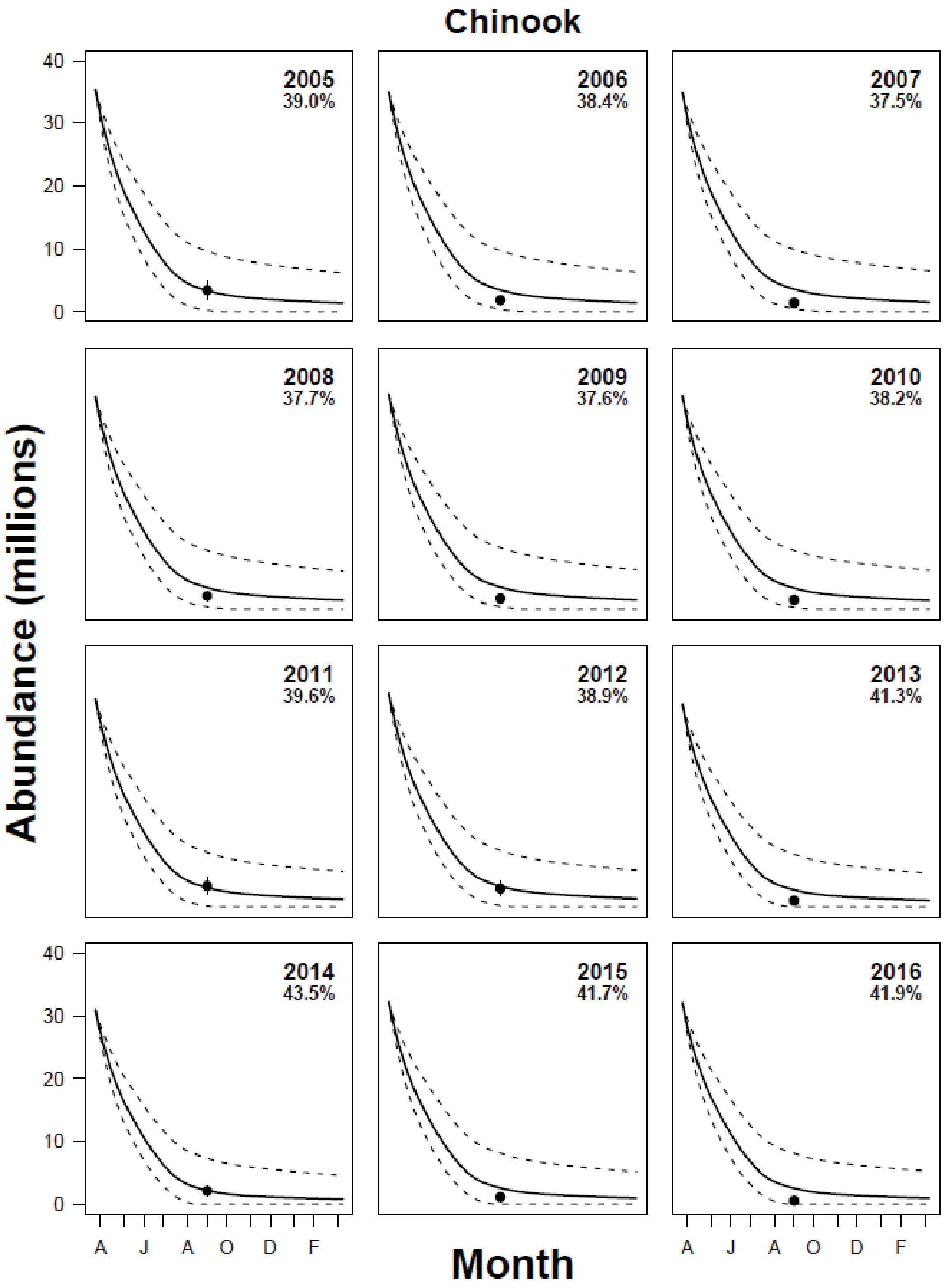

Figure 3.3: Monthly abundance of juvenile Chinook salmon in the Strait of Georgia, from 2004-2016. Solid circles depict the observed abundance in September from annual trawl surveys, with 95% probability intervals shown by vertical black lines. Model-predicted abundance is shown by the decaying black lines, with 95% probability intervals shown by dashed lines. Also shown is the median percentage of the cohort lost to seal predation in the first year.

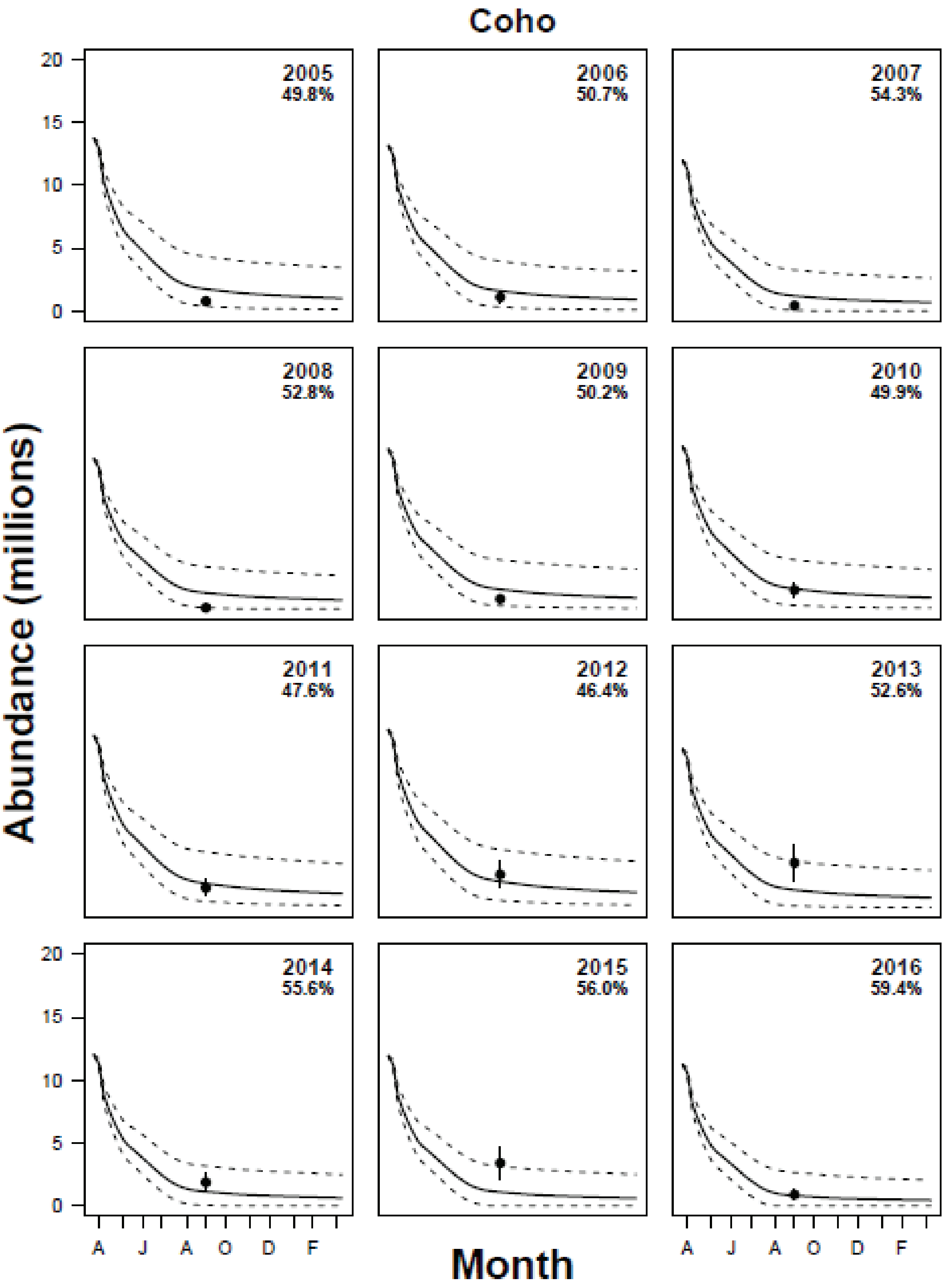

Figure 3.4: Monthly abundance (in millions) of juvenile coho salmon in the Strait of Georgia, from 2004-2016. Solid circles depict the observed abundance in September from annual trawl surveys, with 95% probability intervals shown by vertical black lines. Model-predicted abundance is shown by the decaying black lines, with 95% probability intervals shown by dashed lines. Also shown is the median percentage of the cohort lost to seal predation in the first year.

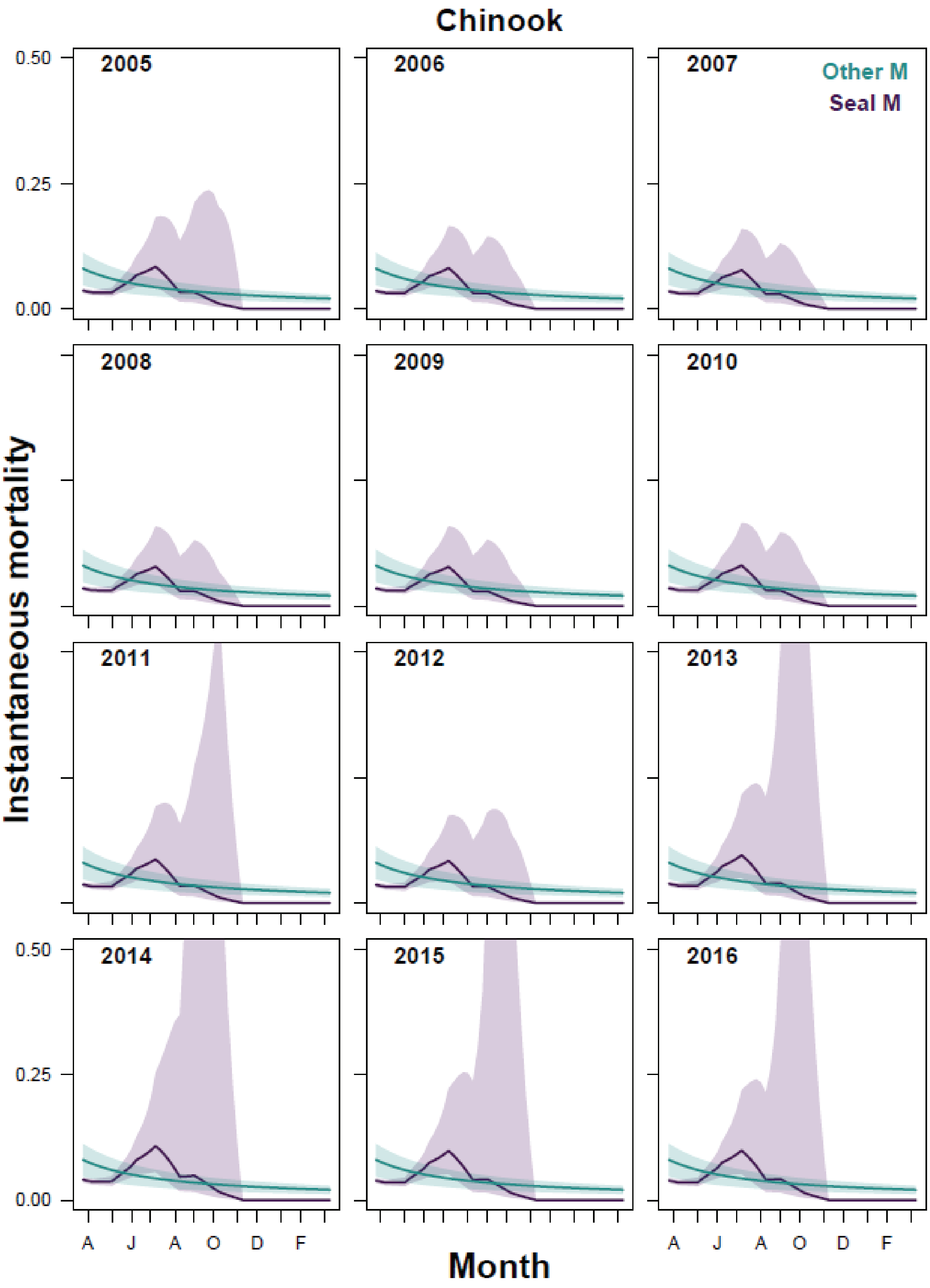

Figure 3.5: Weekly instantaneous mortality rate of Chinook salmon from seal predation (purple) and other sources (teal) in the first year at sea. Solid lines show the median estimate and shaded bands depict the 95% probability intervals.

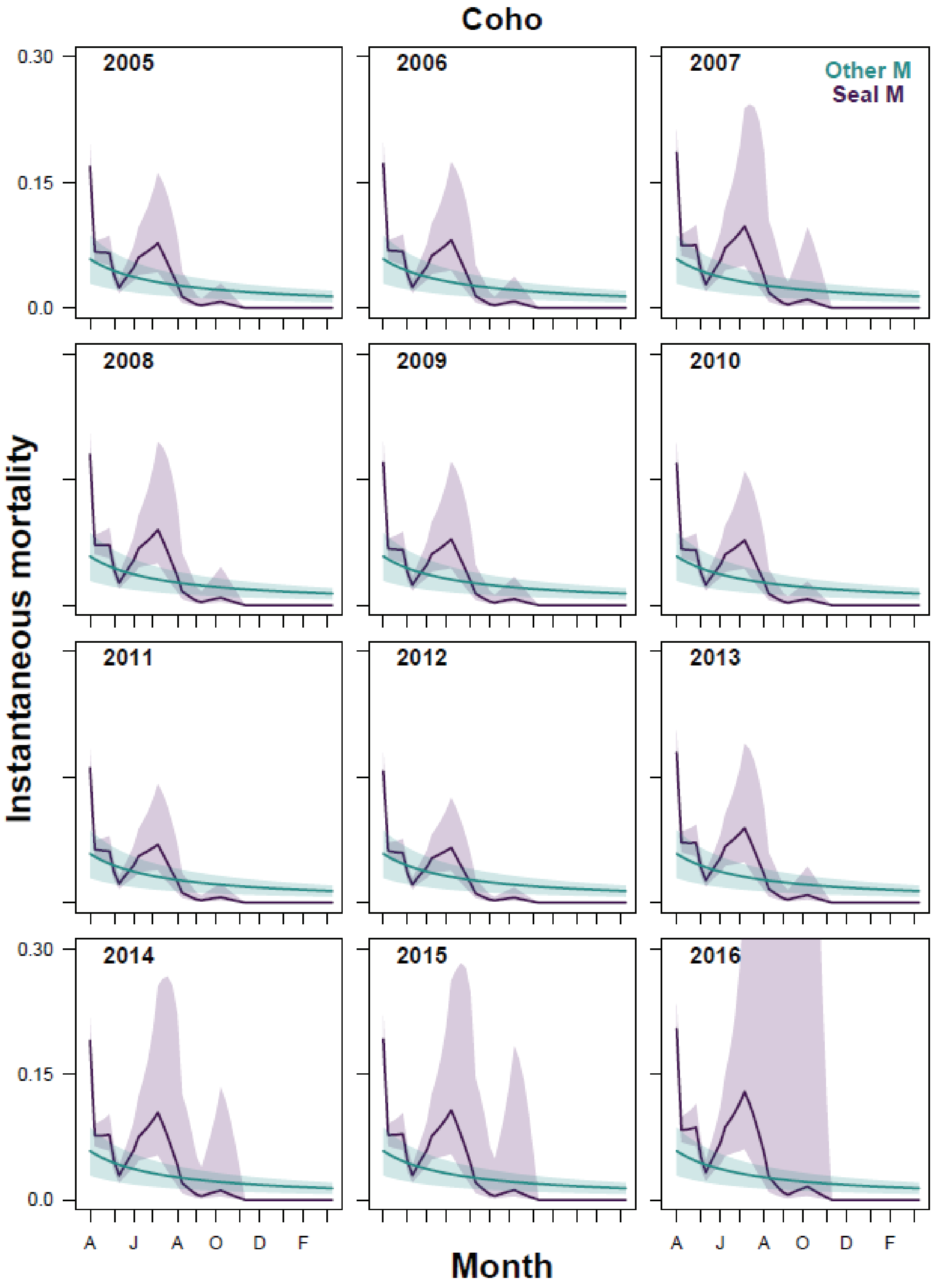

Figure 3.6: Weekly instantaneous mortality rate of coho salmon from seal predation (purple) and other sources (teal) in the first year at sea. Solid lines show the maximum likelihood estimate and shaded bands depict the 95% probability intervals.

Table 3.4: Observed and predicted September abundances of juvenile Chinook salmon in the Strait of Georgia (columns 1-2). Also shown are the annual estimated proportions of each cohort that was lost to seal predation in the first year at sea, the total number of individual Chinook 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. 95% predictive intervals are shown in parentheses for each quantity.

Year	Observed abundance (millions) (95% CI)	Predicted abundance (95% CI) (millions)	Prop. juveniles eaten by seals (95% CI)	Total eaten by seals (millions) (95% CI)	M from seal predation	First year total M
2004	0.98 (0.21-0.57)	3.58 (0.42- 9.51)	0.39 (0.34-0.44)	14.12 (12.23-16.09)	1.24 (0.72- 6.25)	3.19 (1.76- 8.98)
2005	3.45 (2.03-4.87)	3.47 (0.28- 8.84)	0.39 (0.33-0.45)	13.78 (11.74-15.85)	1.24 (0.74- 9.51)	3.19 (1.81-12.35)
2006	1.87 (1.10-2.63)	3.49 (0.41- 9.47)	0.38 (0.33-0.44)	13.36 (11.41-15.47)	1.23 (0.70- 6.26)	3.18 (1.74- 9.04)
2007	1.43 (0.84-2.02)	3.72 (0.42-10.06)	0.37 (0.32-0.43)	13.02 (11.15-15.12)	1.15 (0.66- 5.66)	3.10 (1.67- 8.39)
2008	2.13 (1.25-3.00)	3.48 (0.40- 9.32)	0.38 (0.32-0.44)	12.79 (10.88-14.79)	1.19 (0.67- 5.90)	3.14 (1.71- 8.74)
2009	1.74 (1.02-2.45)	3.63 (0.47- 9.42)	0.38 (0.32-0.43)	12.84 (10.99-14.75)	1.17 (0.68- 4.94)	3.09 (1.69- 7.72)
2010	1.52 (0.89-2.14)	3.42 (0.42- 9.42)	0.38 (0.33-0.44)	12.94 (11.16-14.84)	1.22 (0.68- 6.06)	3.16 (1.71- 8.73)
2011	3.32 (1.95-4.69)	3.12 (0.12- 8.56)	0.40 (0.34-0.46)	13.07 (11.27-15.13)	1.29 (0.73-17.24)	3.30 (2.37- 5.05)
2012	2.93 (1.72-4.13)	3.33 (0.39- 8.79)	0.39 (0.33-0.45)	13.17 (11.22-15.20)	1.25 (0.72- 6.28)	3.22 (2.38- 7.83)
2013	1.00 (0.59-1.41)	2.74 (0.06- 8.06)	0.41 (0.35-0.47)	13.32 (11.44-15.18)	1.42 (0.78-6.34)	3.38 (2.43- 7.70)
2014	2.17 (1.28-3.06)	2.26 (0.05- 7.25)	0.43 (0.37-0.50)	13.39 (11.42-15.52)	1.63 (0.83-7.51)	3.59 (2.49-8.74)
2015	1.19 (0.70-1.68)	2.64 (0.05- 7.93)	0.42 (0.36-0.48)	13.42 (11.51-15.56)	1.46 (0.79-6.92)	3.43 (2.42- 8.85)
2016	0.65 (0.36-0.86)	2.56 (0.05- 7.61)	0.42 (0.36-0.48)	13.35 (11.41-15.26)	1.47 (0.96-4.43)	3.42 (2.44- 5.78)

Table 3.5: Observed and predicted September abundances of juvenile coho salmon in the Strait of Georgia (columns 1-2). Also shown are the annual estimated proportions of each 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. 95% predictive intervals are shown in parentheses for each quantity.

Year	Observed abundance (millions) (95% CI)	Predicted abundance (95% CI) (millions)	Prop. juveniles eaten by seals (95% CI)	Total eaten by seals (millions) (95% CI)	M from seal predation	First year total M
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)

3.5 Discussion

We combined harbour seal diet data from 1,484 faecal samples with a quantitative modeling framework to estimate impacts of predation on juvenile Chinook and coho salmon in the Strait of Georgia, British Columbia. Our analysis suggests that predation by seals during spring and summer could be a significant source of natural mortality for Chinook and coho salmon in their first year of the marine stage — despite these species being a minor component of the harbour seal diet. Our models estimate that harbour seals consumed an annual average of 37-44% of juvenile Chinook salmon (13-14 million fish) and 46-59% of juvenile coho salmon (6-7 million fish) from 2004-2016. These consumption estimates, when combined with abundance data for seals and salmon, suggest mortality rates from seal predation have increased significantly since the 1970s for both prey species. 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 Chinook and coho salmon.

Our study complements previous work on the impacts of harbour seal predation on Chinook salmon in the Salish Sea (Chasco et al. 2017a, b; Thomas et al. 2017), and is the first to quantify possible impacts of pinniped predation on juvenile coho salmon in the Strait of Georgia, at an ecosystem scale. Predation and mortality estimates presented here are potentially useful for quantifying predator-prey dynamics within the context of ecosystem-based fisheries management framework (Marshall et al. 2018a) and ecosystem modeling, in addition to updating current understanding of factors influencing marine survival of Pacific salmon stocks of high conservation concern.

3.5.1 Predation impacts to juvenile Chinook and coho salmon

As shown in previous studies, juvenile Chinook and coho salmon comprise a relatively small fraction of the annual harbour seal diet in the Strait of Georgia and the Salish Sea (Lance et al. 2012; Thomas et al. 2017; Nelson et al., *in review*). 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. b; Nelson et al., *in review*). Despite the fact that neither prey species exceeded 4% of the overall diet in any given month, we estimated that harbour seals consume an average of 37-44% of juvenile Chinook salmon entering the ocean during the spring in the first year at sea. This is somewhat higher than Chasco et al.'s (2017a) estimate of seal predation on Chinook salmon in the Puget Sound (~22%), which may reflect the significantly higher densities of predators in the Strait of Georgia (Chapter 2; Nelson et al. 2019b).

It is important to note that this modeling study and others (Chasco et al. 2017a) assume no movement of Chinook salmon between the Strait of Georgia and Puget Sound, which is surely incorrect. A subsequent study by Chasco et al. (2017b) estimated annual juvenile Chinook salmon consumption by harbour seals for the entire Salish Sea at 8-47 million fish. If we assume consumption of Chinook salmon in the Puget Sound was half of what was estimated in our study (~7 million), the combined estimate of annual consumption (~21 million) for the Salish Sea would fall well within the bounds of Chasco et al.'s (2017b) estimate.

The range of predicted annual mortality from seal predation on Chinook salmon (1.15-1.63; see Table 3.4 and Fig. 3.7) suggests that the regression effect sizes estimated in Chapter 2 are likely unrealistically high. Specifically, the mean effect size of apparent seal predation on wild Chinook stocks in the Strait of Georgia from the previous chapter implies an instantaneous mortality rate of 11.79 (Table 2.4; Fig. 2.4). However, the mean of the lower credible intervals across these stocks imply a predation rate of 1.79 (Table 2.4), which is comparable to the average predation rates estimated in the chapter for juvenile Chinook. Notably, our predicted increases in seal-related mortality from 1970-2016 for juvenile Chinook (1.39) and coho salmon (1.68) are similar to increases in total mortality from another regression analyses using coded-wire-tag data that estimated an increase in total mortality of 1.5 for Chinook salmon and 2.0 for coho salmon (Table B4; PBPS 2019). This comparison suggests increases in the magnitude of seal predation between the 1970s and present day could explain most of the increases in total marine mortality throughout the same time period.

Future research on 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, as some estimates have suggested a large fraction of coho salmon rearing in the Strait of Georgia may be of Puget Sound origin (Beacham et al. 2016). Similarly, the close proximity of the Fraser River delta to north Puget Sound, in addition to the high abundance of natural- and hatchery-origin Chinook and coho salmon emigrating from the Fraser River (Nelson et al. 2019a), suggest that a significant number of Canadian Chinook and coho salmon stocks likely rear in U.S. waters for a substantial period of time. Studies on the movements of individual harbour seals in the Salish Sea ecosystem reveal home ranges of animals that suggest migration across boundaries is common (Peterson et al. 2012)—which could also influence efforts to quantify impacts of predation.

While most recent research efforts related to pinniped predation on salmon in the northeast Pacific and Salish Sea ecosystems have focused on impacts on Chinook salmon, 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 federal, state and provincial protections that Chinook salmon do in the Salish Sea, but it is important to acknowledge their benefit to ecosystem function, as potential prey for southern resident killer whales (*Orcinus orca*) (Ford et al. 2016), in addition to their contribution to indigenous, commercial, and recreational fisheries in the region (Beamish et al. 2010a; Bendriem et al. 2019). Rapid declines in coho salmon abundance have been a major driver for restrictive fisheries policies in the Strait of Georgia and outside waters (Walters et al. 2019).

Our work suggests that harbour seal predation is a significant factor affecting early marine survival of coho salmon in the Strait of Georgia, as our model predicts one out of every two young coho salmon are eaten by seals within the first seven months. 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., *in review*).

3.5.2 Management implications

The seasonal dynamics of seal-related mortality on juvenile Chinook and 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 both species, when large numbers of young salmon—particularly coho salmon—have departed estuarine and nearshore habitats to rear in the offshore pelagic environment. However, relative predation rates appear to be higher upon ocean entry for coho salmon, compared to Chinook as observed in a recent study, where tagged harbour seals along east Vancouver Island responded to pulses of hatchery-released juvenile coho salmon, while ignoring much [numerically] larger releases of Chinook salmon from the same hatchery (Allegue et al. 2020).

Research on foraging patterns, growth, and survival of juvenile Chinook and coho salmon suggest that individuals that survive 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 the late-spring. With these seasonal mortality dynamics in mind, it would appear that management alternatives involving only targeted culls of individual predators within river mouths or estuaries are unlikely to have substantial benefits, due to delayed compensatory mortality that occurs later in the summer. Such policies would be "lose-lose" options that 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 Chinook and coho salmon during the summer months reflects predators targeting young salmon, or is due to temporal and spatial overlap with species like Pacific herring and Pacific hake, which are the preferred prey of harbour seals in the Salish Sea ecosystem (Trites and Rosen 2019; Trzcinski 2020).

3.5.3 Model assumptions and limitations

Despite accounting for uncertainty in several key model inputs and parameters in predation models for both prey species, and confronting those models with an alternative set of equations and predictions, this analysis does have several important limitations. First, the empirical foundation of this study are the estimates of monthly proportions of juvenile Chinook and coho salmon in the harbour seal diet. Accurately quantifying and describing predator diets using DNA and hard structures [extracted from faecal material] is 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).

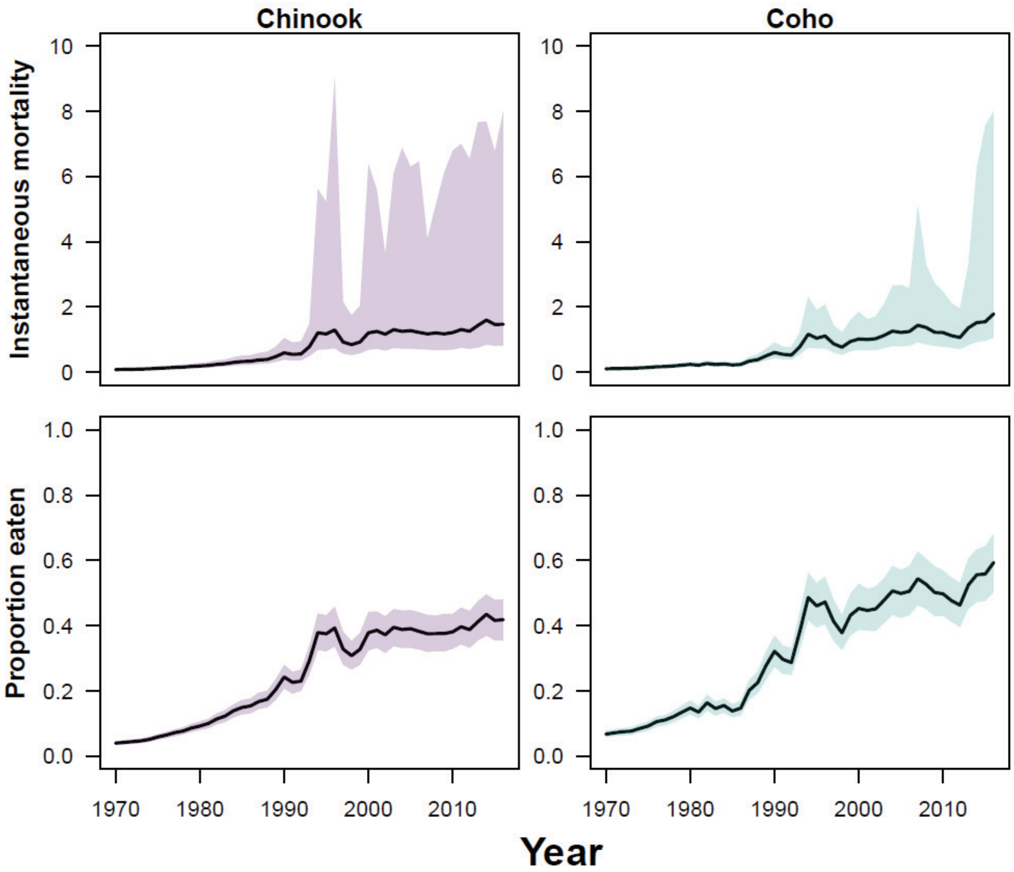

Figure 3.7: Estimated annual total instantaneous mortality from seal predation during the first year at sea (top row) for Chinook and coho salmon, and the proportion of the juvenile cohort lost to seal predation (bottom row) annually in the Strait of Georgia, from 1970-2016. Solid black lines show the maximum likelihood estimates, while the colored bands depict the 95% probability intervals. Note that these projections assume production from natural-origin stocks of Chinook and coho in the Strait of Georgia have remained stationary over time, while hatchery releases have decreased in recent years (see: Fig. 3.2).

While the methods we used represent an improvement from the studies performed almost three decades earlier (Olesiuk et al. 1990), the sampling design used to produce our dataset does introduce potential bias with regards to representation of the harbour seal diet in the Strait of Georgia. Of the four sampling sites we used in our study (Fig. 3.1), two of them (Fraser River and Cowichan Bay) are unambiguously estuarine habitats. The seal haul-out 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 towards animals in estuary sites, which may have higher encounter rates with juvenile salmon because of their close proximity to river mouths. However, it is important to acknowledge that some harbour 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 reveals non-estuary samples have some of the highest proportions of juvenile Chinook salmon of any strata (Thomas et al. 2017). This finding is also consistent with a previous study that documented seal diets in the San Juan Island archipelago in Washington State, located less than 50 km from the Belle Chain islets (Lance et al. 2012). Finally, recent efforts by DFO scientists to test for differences in seal diets between estuary and non-estuary haul-out sites have not found statistically meaningful difference in the proportions of juvenile salmon (Majewski, unpublished data). All told, the combined evidence suggests the data we used are likely representative of the Strait of Georgia harbour seal diet, and could be construed by some as a conservative estimate of salmon predation.

The model-predicted mortality rates shown here require an estimate of the number of young salmon at risk to seal predation each year: the sum of hatchery-origin smolts, which is known from detailed release records, and what we assume is a constant *average* number of naturally-produced salmon originating from tributaries in the Strait of Georgia. Our model projections are quite sensitive to this input and, by extension, the freshwater downstream survival that scales the estimate. Because abundance (i.e., number of fish at risk to predation) is inversely related to seal mortality rates, conservative estimates of freshwater survival rates will likewise predict relatively conservative impacts of predation. While survival no doubt varies considerably by stock and location, our estimates of 50% freshwater survival for Chinook salmon and 70% for coho salmon probably represent conservative estimates. A study that included Fraser River Chinook salmon stocks consistently estimated downstream survival of those populations at less than 50% (Welch et al. 2008), and while stocks in regions like east Vancouver Island probably have higher survival because of their shorter migration distance, they are much lower in total abundance. Likewise, coho salmon survival rates during freshwater migration are also likely much lower than the 70% estimate used here (Bradford 1995; Melnychuk 2009); using lower survival rate estimates would also increase our predation estimates.

Finally, the predation estimates made here and similar studies (Chasco et al. 2017a, b) are sensitive to assumptions about prey size, particularly during the period shortly after ocean-entry, when smolts are relatively small (< 12cm) and growing in mass at exponential rates. Our model assumes that harbour seals in the Strait of Georgia consume juvenile Chinook and coho salmon at an average size equal to those sampled in scientific surveys. In light of previous work that suggests harbour seals may select for larger individual prey relative to available prey (Tollit et al. 1997; Nelson et al. 2019a; Allegue et al. 2020), it is possible that our assumed prey size is biased low (Nelson et al., *in review*). Correcting for this bias would reduce the estimated number of individual salmon eaten annually. However, when we examine the observed prey sizes from a sample of Chinook and coho salmon otoliths recovered from scat samples (see: Fig. 6 in Thomas et al. 2017), it is clear that prey size over time is comparable with our assumed pattern of Chinook and coho salmon growth (Fig. B1-B2).

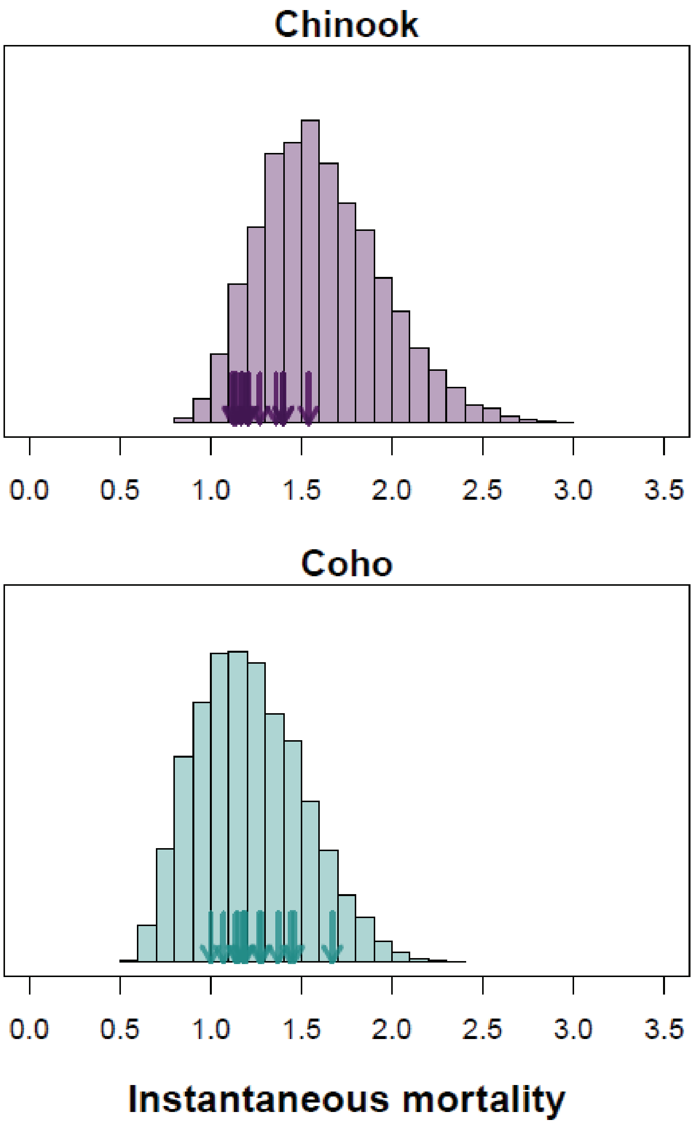

Figure 3.8: "Prior" distributions for seal-related instantaneous mortality rates for Strait of Georgia Chinook and coho salmon during their first year at sea. The histograms (solid bars) for each species are based on 10,000 parameter combinations drawn from the uniform distributions shown in Table B1. Individual arrows along the x-axis show annual median estimates from the predation model for 2004-2016.

3.5.4 Ecosystem considerations

Although multiple model inputs and assumptions contribute to uncertainty in the analysis presented here, our findings provide evidence that harbour seal predation could be an important driver of marine survival during the first year at sea for Chinook and coho salmon in the Strait of Georgia. The recent correlative findings (Nelson et al. 2019b; Sobocinski et al., *in review*), in addition to diet and bioenergetics analyses (Lance et al. 2012; Thomas et al. 2017; Chasco et al. 2017a, b), suggest that population control of predators might facilitate the recovery of Chinook and coho salmon stocks that have experienced chronically low levels of marine survival since the 1980s. While 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. Non-additive or "compensatory" mortality occurs when a prey population's total mortality rate remains unchanged despite decreasing abundance or density of a particular predator (Nichols et al. 1984).

An apparent example of compensatory mortality dynamics in populations of juvenile salmonids was documented in a recent study of out-migrating steelhead in the Columbia River basin (Haesaker et al. 2020). It found that removing avian predators like double-crested cormorants (*Phalacrocorax auritus*) and Caspian terns (*Hyrdoprogne caspia*) did not meaningfully increase overall survival, as fish navigated a gauntlet of potential predators in a heavily altered riverine environment. 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 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 harbour 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 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.

While recent policy discussions about whether to deliberately reduce harbour seal populations in the Strait of Georgia have focused mainly on the quantitative uncertainty about the numbers of young Chinook and coho salmon consumed (Trites and Rosen 2019; Trzcinski 2020), the most important uncertainty about such policies is actually about 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 like disease, high water temperatures, and lack of prey. There is no way, in principal, to resolve this deeper uncertainty by continued predator diet studies and more precise modelling results. Rather, a reduction in seal abundance would be necessary to test whether mortality rates decrease, as predicted. Essentially, any active population control of the harbour 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.

Chapter 4: Comparing lethal and non-lethal methods of active population control for harbour seals in British Columbia, Canada

4.1 Summary

Pinniped populations around the world increased rapidly after hunting and culling during the nineteenth and twentieth centuries ended. Some believe that pinnipeds are now preventing the recovery of certain fish populations, and that one way to recover them might be to control pinniped population abundance using lethal measures such as sustainable harvesting, or by non-lethal means like contraception. However, it is unclear how effective and how long it would take for such methods of population control to bring numbers of pinnipeds down to target levels. We used sex- and age-structured population models to estimate the time it would take to reduce harbour seal (*Phoca vitulina*) numbers in British Columbia by 50% via lethal removals and sterilization of adult females. Simulation modelling suggests reliance on contraception exclusively is unlikely to significantly reduce the current harbour seal population (numbering ~100,000) within a 25-year time horizon, and would result in higher variation around target abundances, compared to lethal removals. However, results suggest contraception could be combined with sustainable harvesting to maintain a target abundance of harbour seals (although captive studies with harbour seals are needed to confirm the efficacy of contraception). Our simulation modeling approach provides a useful framework to assess how non-lethal measures could be integrated into policies that promote active population control of harbour seal numbers, in addition to providing coarse estimates of effort and time required to implement such actions.

4.2 Introduction

The recovery of many marine mammal populations in ecosystems around the world is considered one of the great wildlife conservation success stories in the twentieth century (Magera et al. 2013). Examples are numerous, and include cetaceans (whales, dolphins, and porpoises), pinnipeds (seals and sea lions), and otters (Lotze et al. 2011; Monnahan et al. 2015; Valdivia et al. 2019). While many have celebrated the outcomes of these protections, the recovery of some marine mammal species has presented formidable challenges for managers tasked with recovery of mammals and fish that they prey on (Samhouri et al. 2017). Management conundrums also arise when recovered marine mammal species consume species valued by fisheries (Punt and Leslie 1995; Trijoulet et al. 2017), or compete with other species of high conservation concern (Williams et al. 2011; Chasco et al. 2017b).

Harbour seals (*Phoca vitulina*) are the most widely distributed pinniped species in the world and can be found in temperate and Arctic seas of the Northern Hemisphere. On the west coast of North America, harbour seal populations increased exponentially following protection from hunting and culling in the early-1970s, then leveled off in the 1990s (Jeffries et al. 2003; Brown et al. 2005; Olesiuk 2010). In British Columbia, prolonged hunting and culling efforts in the nineteenth and twentieth centuries were not controlled by any specific management policy, and are believed to have been preceded by some ambient level of hunting by First Nations groups (McKechnie 2013).

Coincident with the recovery of harbour seals in British Columbia were declines in marine survival of some stocks of Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), and steelhead (*O. mykiss*) (Zimmerman et al. 2015; Nelson et al. 2019b; Sobocinski et al. 2020). Chinook and coho salmon are valuable components of fisheries (commercial, recreational, and indigenous), and are of high cultural significance to indigenous North Americans. Arguably, the most important role of Chinook salmon serve in the ecosystem today is prey for resident killer whales (*Orcinus orca*), an ecotype of killer whales that specialize almost exclusively on adult Chinook salmon (Ford et al. 2016). Southern resident killer whales—a distinct group of fish-eating killer whales—are currently listed as “endangered” in Canada (Species at Risk Act) and the United States (Endangered Species Act), and the recovery of Chinook salmon is believed to be of high importance to reducing their risk of extinction (Wasser et al. 2017). In response to the perceived impact of predation on Chinook salmon populations, and the potential competition with southern resident killer whales, some stakeholders have advocated reducing the abundance of harbour seals in British Columbia and Washington State (USA) through permitted culling and/or sustainable harvest (Southern Resident Orca Task Force 2018; PBPS 2019).

The large numbers of harbour seals killed in British Columbia before federal protection in the 1970s demonstrates that this population could likely be effectively controlled through intensive harvest (Olesiuk 2010). However, there are several reasons why using lethal measures exclusively may not be desirable. For example, the Strait of Georgia has the highest densities of harbour seals in the province (Olesiuk 2010), but its proximity to major population centers (Vancouver and Victoria) and recreational areas could pose unacceptable risks to human safety. Additionally, wildlife managers may lack the political will to undertake such a policy because of the ethical issues associated with large numbers of lethal removals (Lavigne 2003). Similarly, embarking on a policy of active population control using lethal measures would likely be met with litigation from animal welfare and conservation interests. Thus, solutions that reduce seal abundance or curtail reproduction that do not involve lethal methods of population control could be of interest to managers.

Fertility control of terrestrial mammal species has been implemented in many ecosystems as an alternative or complimentary management strategy to hunting and culling, and is viewed by some as a humane means of controlling wildlife populations (Kirkpatrick and Turner 2008; Carroll et al. 2010; Messai and Cowan 2014). There has been growing interest in the scientific literature on the subject of fertility control in wildlife populations, with the most common application in mammal species being immuno-contraceptive vaccines that are intended to sterilize females. Species where such methods have been applied include rabbits, possums, badgers, foxes, cats, dogs, pigs, deer, elk, bison and horses. Applications to these wild populations have been successfully achieved in Asia, North America, and Australia (Messai and Cowan 2014).

Research has shown that a considerable initial investment of effort and resources is necessary to achieve meaningful reductions in fertility in wild populations, if immuno-contraceptive methods are used exclusively. Large field applications have also yielded mixed results, ranging from completely unsuccessful (Twigg et al. 2000; Williams et al. 2007) to marked reductions in abundance and population growth rate (Kirkpatrick and Turner 2008; Rutberg and Naugle 2008).

Among pinnipeds, two primary forms of contraception have been previously explored, mainly for application in captive populations. These include injection of exogenous sex hormones that interrupt ovulation, and vaccine administration (*zona pellucida* antigens) that trigger an autoimmune response directed at the ova, which in turn prevents fertilization (Dierauf and Gulland 2001). Single-administration *zona pellucida* vaccines have been successfully used on wild grey seals (*Halichoerus grypus*) in the Atlantic Ocean (Sable Island, Nova Scotia), which resulted in reduced pup production among treated animals by around 90% (Brown et al. 1997). This immuno-contraceptive was further found to be effective over a wide range of ages, although it was unclear how quickly efficacy of the vaccine diminished after it was administered. *Zona pellucida* has not yet been administered to harbour seals in an experimental setting, but is expected to result in similar outcomes to those seen in grey seals (M. Fraker, SpayVac®, Inc., Victoria, B.C., Canada, pers. comm.).

Before allocating resources to test the efficacy of *zona pellucida* on harbour seals, the potential outcomes of large-scale applications of this contraceptive should be evaluated and compared with lethal methods used in the past (i.e., indiscriminate culling and hunting). One way of doing so is by combing population models fit to data with simulation models, which has been done to estimate the effects of fertility control in pig and horse populations (Ballou et al. 2008; Raiho et al. 2015; Pepin et al. 2017). Such approaches can explicitly incorporate uncertainty into key system inputs and parameters to evaluate model predictions and management outcomes.

Using both simple logistic growth models, and age- and sex-structured models of the harbour seal population in British Columbia, we compared expected outcomes of lethal (sustainable harvesting) and non-lethal (sterilization by immuno-contraception) population control. The primary goal of our analysis was to compare an alternative form of population control to the management alternative of indiscriminate harvesting that has been proposed. Performance measures for management actions include the expected duration of actions necessary to achieve a desired predator abundance, and the level of effort needed to maintain the target abundance.

4.3 Methods

4.3.1 Harbour seal data

We used estimates of total seal abundance, historical kill records, and estimates of population age-composition to develop an age- and sex-structured population dynamics model of the harbor seal population in British Columbia. A total of 19 abundance estimates were available from aerial surveys of harbour seal haul-outs in British Columbia, which were performed periodically between 1973 and 2014 (Olesiuk 2010; Majewski and Ellis, *in review*) (Table 4.1). Kill records from hunting and culling programs in the late-nineteenth and twentieth centuries were compiled from various sources as summarized by Olesiuk (2010). Because the number of recorded pelts and bounties likely underestimated the number of animals actually killed due to unrecoverable carcasses, Olesiuk (2010) assumed 62% of animals killed were accounted for. Additionally, since the number of animals reported killed via programmatic culling was likely overestimated (i.e., all animals shot did not necessarily die), the study assumed a kill probability of 75% (Olesiuk 2010). Seal pups were likely to have been more vulnerable to harvest than older individuals (Bigg 1969; Olesiuk 2010), so we assumed different vulnerability parameters for pups and non-pups (Table 4.2). Finally, we used age-composition estimates for seals shot during a period of intensive culling in the 1960s, which were based on analysis of canine teeth from 324 animals sampled during these hunts (Bigg 1969). These three datasets, along with prior distributions on several parameters, were used to fit the population model using a Bayesian approach, which is described in the following sub-section.

4.3.2 Population dynamics models

The primary population dynamics model developed for this study is a state-space age- and sex-structured model that estimates the total abundance of each age-sex group on an annual time step between 1880 and 2018. The state-space framework used here allows us to explicitly account for error associated with the observation of the abundance data, in addition to process error, which we assume enters the population model in the form of annual recruitment deviations. In addition to the full sex- and age-structured model, we developed a simpler logistic growth model for the harbour seal population, which we fit to the same abundance data. This was done to evaluate whether sufficiently similar results could be obtained using a logistic model that was fitted to the same abundance data, and applied to evaluate the effectiveness of the alternative harbor seal control options. The details of the logistic model are described in Appendix C, and we include a comparison of the two model formulations in the Results section of this chapter.

Table 4.2 summarizes the symbology of estimated and fixed parameters used in the full age-structured model, in addition to the subscripts associated with model parameters and variables. The maximum age for each sex (A^s) was assumed to be 25 for females and 15 for males; the small numbers of animals thought to be older were assumed to fall into these “plus groups”. We assumed the harvested population in 1880 was at a stable age distribution and initialized the population model with the following equations:

(Eq. 4.1)
$$N^s_{1,a} = \gamma^s N_{1879} s_a^{s(a-1)} (1 - s_a^s)(1 - v_a U_t) \qquad 1 \leq a < A^s$$

(Eq. 4.2)
$$N^s_{1,a} = \gamma^s N_{1879} s_a^{s(A-1)} (1 - v_a U_t) \qquad a = A^s$$

where v_a and U_t are the vulnerability at age and harvest rate in year t. γ^s is the proportion of the population of sex s at equilibrium: $\gamma^s = \frac{\sum_{a=0}^{A} l_a^s}{\sum_s \sum_{a=0}^{A} l_a^s}$. Here, l_a^s is the survivorship of animals of sex s at age a:

(Eq. 4.3)
$$l_a^s = \begin{cases} 1 & a = 0 \\ l_a^s = l_{a-1}^s s_{a-1}^s & 0 < a < A^s \\ l_a^s = l_{a-1}^s s_{a-1}^s & a = A^s \end{cases}$$

Annual survival for pups (s_0=73%), females (s^{Female}=90%), and males (s^{Male}=85%) were assumed to be constant over time, and known from previous estimates from tagging studies in the literature (Olesiuk 1993). Because tagging studies such as these are susceptible to bias from issues like tag shedding, and because natural mortality can be non-stationary over time, we also evaluated two alternative models: 1) a version with female and male survival rates 25% greater than the nominal rates, and 2) a version with 25% less than the nominal survival rates.

The population model was projected forward from initial conditions with the following set of equations:

(Eq. 4.4)
$$N_{t+1,a+1}^s = \begin{cases} N_{t,a}^s s_a^s (1 - v_a U_t) & 1 \leq a < A^s \\ \left(N_{t,a}^s + N_{t,a-1}^s\right) s_a^s (1 - v_a U_t) & a = A^s \end{cases}$$

The annual harvest rate was calculated using the equation:

(Eq. 4.5)
$$U_t = \frac{C_t}{N_t}$$

where C_t is the number of animals killed in year t, which is assumed to be known exactly from published estimates described above (Olesiuk 2010). To improve the stability of the model-fitting process, we assumed a minimum annual harvest rate of 0.001. The maximum annual harvest rate was limited to 0.90.

Table 4.1: Estimated and observed annual abundances of harbour seals in British Columbia, Canada between 1973 and 2014. Observed abundances were calculated from aerial survey data in Olesiuk (2010) and adjusted by the observability coefficient (*q*), while estimated abundances were taken from the best-performing age-structured population model.

	Abundance	
Year	**Estimated (95% CI)**	**Observed/*q***
1973	11,991 (8,723-15,258)	10,068
1974	13,042 (9,771-16,314)	11,105
1976	15,470 (12,975-17,966)	13,834
1982	25,823 (21,607-30,039)	25,336
1983	28,114 (23,882-32,346)	28,151
1984	30,602 (26,198-35,007)	31,346
1985	33,289 (27,836-38,742)	34,334
1986	36,189 (31,026-41,352)	37,620
1987	39,311 (33,463-45,160)	42,436
1988	42,635 (35,401-49,869)	46,512
1990	49,919 (43,555-56,284)	56,998
1992	57,888 (47,840-67,936)	58,842
1994	66,469 (54,991-77,947)	76,423
1996	74,859 (67,518-82,200)	80,610
1998	82,342 (74,099-90,585)	75,817
2000	88,426 (78,495-98,356)	87,624
2003	93,792 (85,619-101,964)	93,268
2008	96,606 (88,584-104,627)	93,692
2014	97,537 (88,438-106,637)	99,345

Annual pup production was assumed to be the density-dependent process limiting population growth, and was described by a theta-logistic/Pella-Tomlinson relationship (Pella and Tomlinson 1969), where the number of pups that enter the population annually is a function of total abundance relative to population carrying capacity. We believe this is a reasonable assumption, as population growth is likely limited by suitable habitat and/or prey availability (Brown et al. 2005), and because it is well-documented that pup production/survival in pinniped populations is often inversely related to animal density at haul-outs and pupping areas (Coulson and Hickling 1964, Bigg 1966). We assumed a 1:1 sex-ratio for pup production in each year (Bigg 1969):

(Eq. 4.6)

$$N_{t,0}^{s} = 0.5\left(F_t \sum_{a=1}^{A^{Female}} f_a N_{t,a}^{Female}\right)$$

where f_a is the fecundity at age (Table 4.2), and F_t is the time-varying birth rate:

(Eq. 4.7)

$$F_t = \left[\left(1 - \frac{N_{t-1}}{K}\right)^{\theta}\right] exp(\varepsilon_t)$$

Here, K is the population carrying capacity, θ is the parameter that controls the strength of density-dependence, and ε_t is the annual recruitment deviation, which were assumed to be normally distributed: $\varepsilon_t \sim Normal(0, \sigma_{Rec})$. Recruitment deviations were only estimated for pup production between 1940 and 2018, as the first year of observed data (age-composition) wasn't available until the mid-1960s. To limit the amount of process error, we set σ_{Rec} to 0.075, which is comparable with levels of annual recruitment variation in other seal populations (Øigård and Skaug 2015). In addition to Eq. 4.7, we also evaluated an alternate pupping function:

(Eq. 4.8)
$$F_t = \left[1 - (1 - F)\left(\frac{N_{t-1}}{K}\right)^{\theta}\right] exp(\varepsilon_t)$$

where F is the pupping rate at carrying capacity (K) (Skaug et al. 2007). Versions of the age-structured model that used Eq. 4.8 were found to be far less stable during the model-fitting process (described below), and did not consistently produce valid parameter estimates. Thus, from this point forward, we only discuss methods and results using versions of the age-structured model that incorporate Eq. 4.7 as a pupping function.

4.3.3 Parameter estimation

We fit our state-space models to the abundance, age-composition, and harvest data by minimizing the objective function described below, which is comprised of the sum of two likelihood terms and the prior distributions specified above: $(L_1 + L_2 + priors)$. For the observation model, we assumed the natural log of the abundance estimates were normally distributed with the following log-likelihood:

(Eq. 4.9)
$$L_1 = -nlog_e(\sigma_{Obs}) + c_1$$

where c_1 is a component of the lognormal log-likelihood that remains constant at different parameter values and can be ignored; σ_{obs} is the observation error standard deviation:

(Eq. 4.10)
$$\sigma_{Obs} = \sqrt{\frac{\sum_{i=1}^{n} log_e(x_i/q\,/N_i)^2}{n}}$$

where x_i is the observed total abundance, N_i is the predicted total [non-pup] abundance from the population model described above, *n* is the number of abundance observations, and q is the "observability coefficient" for the abundance of harbour seals:

(Eq. 4.11)
$$q = exp\left[\frac{\sum_{i=1}^{n} log_e(x_i/N_i)}{n}\right]$$

A normal prior distribution of 1.0 was imposed on q, assuming a standard deviation of 0.15. Age-composition data from lethal sampling efforts in the 1960s (Bigg 1966, 1969) were incorporated into the likelihood function by assuming the observed proportions at age follow a multinomial distribution. Although the samples were collected over several consecutive years, we assumed all samples were from 1965, because only the aggregate proportions were reported:

(Eq. 4.12)
$$L_2 = -\sum_{s} \frac{25}{x_{1965}^{s}} \sum_{a=1}^{A^s} x_{1965,a}^{s} log\left[N_{t,a}^{s}\left(\sum_{a=1}^{A^s} N_{1965,a}^{s}\right)^{-1}\right] + c_2$$

where c_2 is a component of the multinomial log-likelihood that remains constant at different parameter values and can be ignored, and $x_{1965,a}^{s}$ are the observed numbers of animals for each sex, and age class from the lethal sampling circa 1965. To account for the fact that these samples were likely not random (e.g., bias in behavior of captured animals), we assumed an effective sample size of 25 animals (Skaug et al. 2007), which is far lower than the actual number of samples, but large enough to influence the log-likelihood. The objective function was minimized using the 'mle' function ("BFGS" algorithm) in the 'stats4' package in the R Programming Environment (R Core Team 2017).

4.3.4 Comparison of lethal versus non-lethal population control

We used the posterior parameter estimates from the age-structured population model to simulate future harbour seal population dynamics over a range of active population control scenarios. Two general population control methods were tested: 1) indiscriminate lethal harvest of both pups and adults, and 2) contraceptive measures through vaccination of adult females.

When simulating future population dynamics, we assumed the annual recruitment deviates were auto-correlated through a first-order auto-regressive process, which was modeled by: $\epsilon_t = \rho\epsilon_{t-1} + u_t$, where $u_t \sim N(0, \sigma_{Rec})$ and ρ=0.70 (Øigård and Skaug 2015). A total of 1000 simulations were performed for each scenario.

4.3.4.1 Lethal removals

In future projections of lethal management actions, we assumed animals were killed at random, with no age-specific assumptions about vulnerability (pups=1.0; non-pups=1.0). Here, we make no specific recommendation or assumptions about how lethal removals are made (e.g., clubbing, shooting), but we do assume that the total number of removals under each scenario is executed without error.

4.3.4.2 Contraception

For simplicity, and because no long-term studies were available, we assumed sterilization lasts the entire lifetime of a treated animal, which is plausible, based on studies of similar contraceptive agents on other species (Dierauf and Gulland 2001). Further, it was assumed that treatments are applied randomly across all non-pup age classes, and that all treated animals are marked, so that re-treatment will not occur. We assumed that the treated population of females experienced a 90% reduction in fecundity, and that the effect was the same across all age classes (Brown et al. 1997). Essentially, these scenarios depict the most optimistic outcomes, in terms of implementation efficacy, and results should be interpreted as a "best case" scenario.

For the time period after contraception has commenced, annual pup production is calculated by modifying Eq. 4.7:

(Eq. 4.13)
$$N_{t,0}^{s} = 0.5\left[\left(F_t \sum_{a=1}^{A^{Female}} f_a N_{t,a}^{Female}(1-p_t)\right) + \left(F_t \sum_{a=1}^{A^{Female}} f_a^* N_{t,a}^{Female} p_t\right)\right]$$

where p_t is the proportion of females treated in year t, and f_a^* is the altered fecundity schedule for treated animals. The proportion of treated females in the population is $N_t^{Sterile}/N_t^{Female}$, where the number of treated females in the population is

(Eq. 4.14)
$$N_t^{Sterile} = \begin{cases} V_t s^{Female}, & t = 2019 \\ \left(N_{t-1}^{Sterile} + V_t\right)s^{Female}, & t > 2019 \end{cases}$$

$V_{t,a}$ is the number of females (non-pups) treated in year t, which are subject to the same annual survival rate as untreated animals. For the purposes of this simulation, we did not track the age-structure of the vaccinated female sub-population separately.

4.3.4.4 Management scenarios

Under both lethal and non-lethal management options, we simulated the population dynamics of the harbour seal population over multiple levels of effort. For lethal measures (i.e., indiscriminate lethal removals), we assumed the maximum number of animals that could be killed annually was comparable to the maximum observed harvests in the historical records, which was around 16,000 animals per year (Fig. 4.1). For contraception of females (vaccination), we assumed the maximum effort could be 10,000 animals, which is likely far higher than would be logistically feasible (S. Jeffries, Washington Dept. of Fish and Wildlife, Olympia, WA, USA, pers. comm.). We evaluated scenarios where exclusively lethal or exclusively non-lethal methods were used, as well as scenarios that used a combination of both methods from the start of the management period. For each scenario, we calculated the mean number of years necessary to achieve the target abundance for the harbour seal population, which we set at 50,000 adult animals. We selected this target based on the abundance of seals desired by some stakeholders in British Columbia (PBPS 2019).

For scenarios where a combination of both lethal and non-lethal methods were used, we evaluated two different implementations: 1) a combination of lethal and non-lethal efforts occur simultaneously from the start of the management period, and 2) an approach in which lethal harvesting was used exclusively until the seal population was depleted to the target abundance, after which contraception was performed in an attempt to maintain the target abundance through non-lethal efforts. The second approach was added to the analysis after preliminary simulation results suggested depletion of the seal population using contraception exclusively would require a very large number of vaccines, which could be cost-prohibitive. Previous research on terrestrial species has shown more realistic management scenarios may involve using contraception to suppress or maintain a population previously depleted through culling (Raiho et al. 2015).

In addition to the total abundance of the harbour seal population, we also assessed the change in biomass of the daily prey requirement for the total population (B_t) in response to the management scenarios described above. This was achieved by multiplying the simulated abundance of each sex-age group by their respective daily prey requirements (D_a^s), which are available from previous studies in the Strait of Georgia, British Columbia (Olesiuk 1993; Fig. C1):

(Eq. 4.15)

$$B_t = \sum_s \sum_{a=1}^{A^s} N_{t,a}^s D_a^s$$

Table 4.2: Summary of parameters used in the sex- and age-structured population model for harbour seals in the Strait of Georgia. Literature sources for fixed parameter values are listed in the fourth column.

Type	Symbol	Value	Description	Source
Estimated parameters	K	-	Carrying capacity	-
	N_{1879}	-	Abundance in 1879	-
	$\epsilon_{1940-2018}$	-	Recruitment deviates	-
	θ	-	Pup production shape parameter	-
Fixed parameters	$v_a^{Pre-1915}$	1.0, 0.50	Vulnerability for pups and non-pups before 1915	Bigg 1969, Olesiuk 2010
	$v_a^{Post-1915}$	1.0	Vulnerability (pups and non-pups) after 1915	-
	A^s	15, 25	Male and female max. lifespan (i.e., plus group)	Bigg 1966,1969
	s^{Female}	0.90	Female survival	Olesiuk 1993
	s^{Male}	0.85	Male survival	Olesiuk 1993
	s^{Pup}	0.73	Pup survival	Olesiuk 1993
	f_a	0.0 (age 1-3); 0.29, 0.66, 0.79, 0.91 (ages 4, 5, 6, 7-30)	Fecundity at age	Olesiuk 1993
	σ_{qmle}	0.05	q_{mle} prior SD	-
	σ_{Rec}	0.075	Recruitment deviate SD	-
	ρ	0.70	AR(1) term for recruitment deviates	Øigård and Skaug 2015
Subscripts	t	1880:2018	Year	-
	s	Female, Male	Sex	-
	a	1:A^s	Age	-

Since daily prey biomass is a function of the energetic content of the prey composition (Rosen and Trites 2000), the assumption made here is that the prey composition used to estimate daily prey biomass in Olesiuk (1993) has not meaningfully changed. Agreement between two studies from the Salish Sea—which use diet data from different regions (Strait of Georgia vs. Puget Sound) and decades (1980s vs. 2000s)—suggests this is a reasonable assumption.

4.4 Results

4.4.1 Seal population dynamics

According to Akaike Information Criterion (AIC) (Burnham and Anderson 2002), the best age-structured model used a value of 0.50 for the vulnerability of non-pups (before 1915), which will be referred to hereafter as the "base case" age-structured model (Fig. 4.1; Table 4.1). Nine different models were evaluated, with different assumptions regarding harvest vulnerability before and after 1915 (Table C1). The alternative age-structured model, which assumes a non-pup natural mortality rate that is 25% less than the base case model, tracked the dynamics of the base case model from the first year (1870) of the time series through the mid-1990s, at which point the total abundance began to approach an asymptote (Table 4.3; Fig. C2). The total abundance of the alternative model stabilized at a lower population size compared to the base case model, but the mean abundances between 1995 and 2018 still overlapped with the 95% probability intervals for the estimated abundance of the base case model (Fig. 4.1 and Fig. C2). For example, the estimated abundance in 2018 from the alternate age-structured model was 90,233, compared to 97,767 animals predicted by the base case model (Fig. 4.1).

When fit to the same abundance data as the full base case age-structured model, the best-performing theta-logistic model showed the same general population dynamics from 1940-2018 (Fig. C2). A theta-logistic model with θ as an estimated free parameter out-performed the basic logistic growth model where $\theta = 1$ (Table C4). Uncertainty around annual population size in the decades prior to and up until the mid-1960s was considerably higher for the theta-logistic model estimates compared to the full age-structured model—this is likely the result of the lack of age-composition data. While current abundance estimates of the seal population were very similar for both model structures, the age-structured model estimated a higher carrying capacity relative to the theta-logistic model (Table 4.3 and Table C5; Fig. C2).

Table 4.3: Parameter estimates for two sex- and age-structured harbor seal population models. The marginal posterior estimates and standard deviations (SD) are shown for the base case model, which assumes non-pup natural mortality rates reported in Olesiuk (1993), and for an alternative hypothesis where natural mortality of non-pups is 25% less than the literature value. An additional model (+ 25% natural mortality) was also tested, but was not able to produce a stable solution. Standard deviations for each parameter estimate are shown in parentheses, except for q_{mle}, which has a closed-form solution.

Parameter	Base case	-25% M	+25% M
K	117,673 (10,570)	109,190 (9,997)	-
N_{1879}	49,825 (3,745)	44,832 (3,018)	-
θ	2.97 (0.27)	1.87 (0.32)	-
q	1.08	1.15	-

Using the base case age-structured model, the estimated mean population size in 1879 was 49,825 seals (95% PI: 42,485-57,165) (Fig. 4.1). The seal population reached its minimum abundance in 1967 at 8,149 animals (95% PI: 5,391-10,906), a consequence of the very high harvest rates that occurred throughout the decade. The current (2018) estimated abundance of harbour seals in British Columbia is 97,767 animals (95% PI: 87,553-107,982), and the estimated carrying capacity of the population is 117,673 (95% PI: 96,955-138,390), which implies the current abundance is at 83% of carrying capacity. The process error in the base case age-structured model (i.e., the recruitment deviates) was highest as the population grew rapidly between 1970 and the 1990s (Fig. C3). Interestingly, the estimated observability coefficient, q_{mle}, for all three models was greater than 1.00, which implies that either aerial surveys over-counted the actual numbers of adult harbour seals in the survey area or the factor applied by DFO to convert counts to the total population was positively biased. Previous research suggests that potential sources of observation error could be from immigration/emigration, and/or inclusion of pups in the adult counts (Olesiuk 2010).

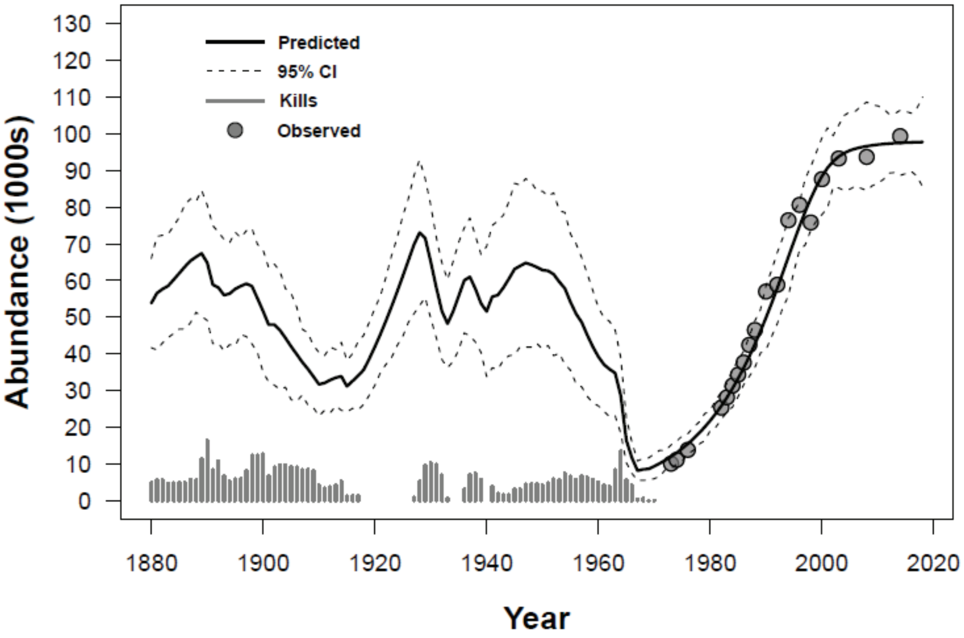

Figure 4.1: Predicted (solid line) and observed (circles) abundance of harbour seals in British Columbia, from 1880-2018. The 95% probability intervals for estimated abundance are depicted by the dashed lines. The number of annual kills (bars) from records of hunting and culling (Olesiuk 2010) are shown along the x-axis.

Once the population was protected from hunting and culling, the ratio of females to males in the population increased steadily, with the current sex ratio estimated to be 59.6% females and 40.4% males (Fig. 4.2). The estimated population proportions at age in 1965 showed a good fit to the observed data for both females and males (Fig. 4.3). The average age of non-pups in the population increased following cessation of harvesting in the early-1970s, as the proportions of young animals began to decline (Figs. 4.4-4.5). Specifically, the average age of adult females increased from 9.2 to 11.5 years, while the average age for males went from 6.1 to 7.4 (Fig. 4.5). The maximum estimated harvest rate for harbour seals in British Columbia occurred in 1964 at 47.2% (Fig. 4.4). It is estimated that birth rates were highest during periods of intense harvest, but declined steadily once the population was protected in the 1970s (Fig. 4.5). Average age has been stable since the 2010s for males, while the average age of females appears to still be increasing (Fig. 4.5).

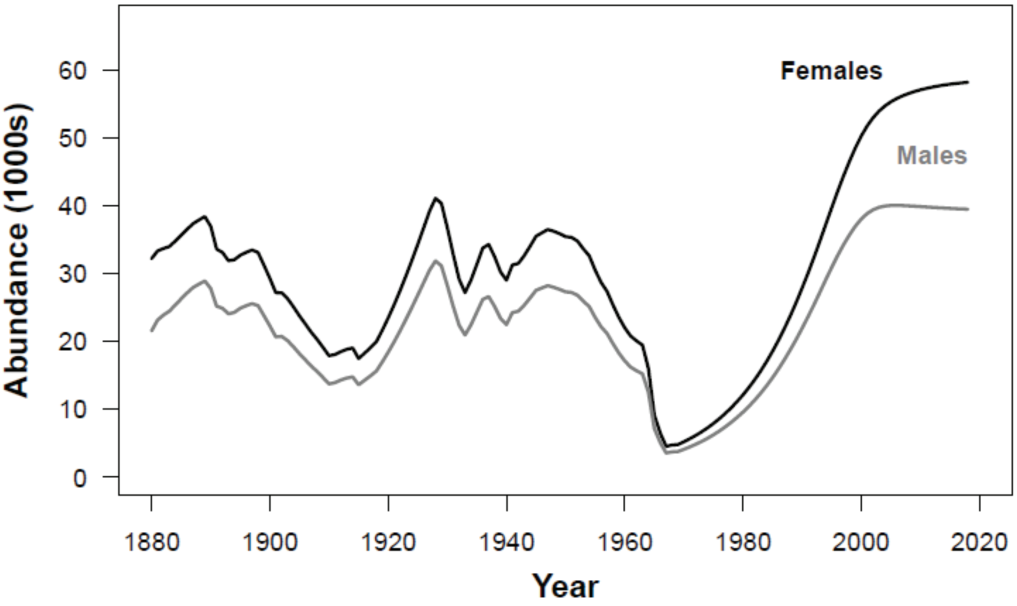

Figure 4.2: Model-predicted abundances of female (black) and male (gray) harbour seals in British Columbia, from 1880-2018.

4.4.2 Comparison of management alternatives

The future population dynamics of the harbour seal population were simulated under nine different scenarios of active population control: three scenarios using varying levels of indiscriminate harvesting exclusively, three using fertility control exclusively, and three using a combination of lethal measures and fertility control from the first year of the management period

(Fig. 4.6). Simulations of these nine scenarios suggest that adoption of indiscriminate harvesting as a management alternative would require considerable effort to achieve the target depletion level (50,000 animals) within 10 years (Fig. 4.6). For example, a simulated annual removal of 5,000 animals failed to achieve the target population level within 25 years (Figs. 4.6-4.8). On average, an annual removal of 9,000-10,000 animals would be required to reduce the seal population to the target abundance within a decade (Figs. 4.6-4.8). Annual removals of 15,000 animals per year, which would be comparable to the annual largest efforts during the twentieth century, would reduce the population to the target abundance within approximately five years, on average (Fig. 4.7). Using non-lethal measures exclusively, between 4,000-5,000 females would need to be vaccinated annually to achieve the target abundance within 25 years (Figs. 4.7-4.8). Approximately 7,500 females, on average, would need to be vaccinated annually to reach the target abundance in 15 years. Once annual vaccination efforts reach 7,000-7,500 females per year, there is a clear level of diminishing returns, with regard to decrease in population level per vaccination (Fig. 4.7).

Management scenarios involving a simultaneous combination of sustainable harvesting and fertility control reduced the number of years necessary to achieve the target abundance, compared with those only using lethal methods. (Fig. 4.6-4.7). For example, while indiscriminate harvesting of 5,000 animals a year would fail to achieve target abundance within 25 years, such an effort that is augmented with the vaccination of 2,500 females would achieve the target population abundance in approximately 15 years (Fig. 4.6). Similarly, an annual combination of 5,000 culls and 5,000 vaccinated females would achieve target abundance within approximately 10 years of management (Fig. 4.6-4.7). When non-lethal methods were applied *after* the target abundance has been achieved through harvesting, moderate levels of contraception were required to maintain the population below or at the target abundance (Fig. 4.9). Scenarios where 2,500 vaccines were applied annually following a period of harvesting failed to maintain the seal population at target abundance, and the population steadily recovered, albeit to a lower level (Fig. 4.9). It appears that annual efforts involving the vaccination of at least 5,000 females would be required for scenarios where fertility control was implemented after target abundance was reached through harvesting.

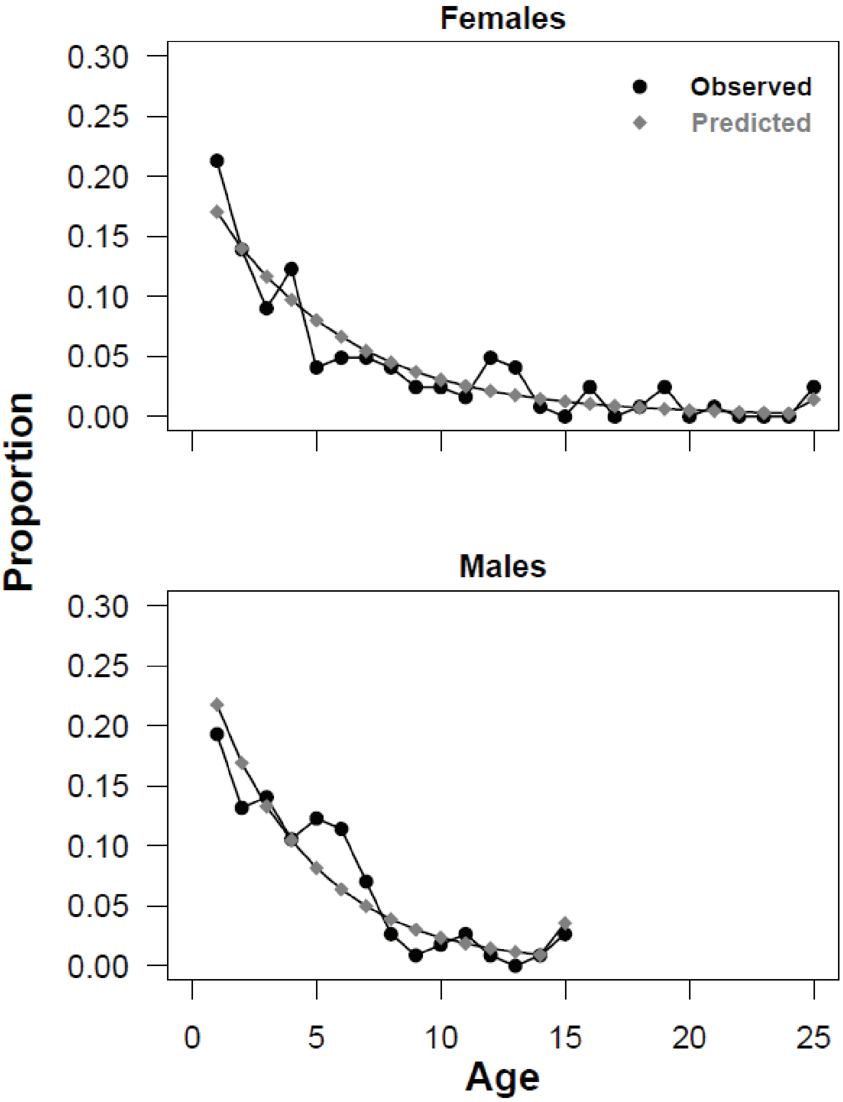

Figure 4.3: Predicted (grey) and observed (black) age-composition of the harbour seal population (non-pups) in 1965 for females (top panel) and males (bottom panel).

While augmenting lethal approaches with non-lethal contraceptive methods did result in faster depletion of the seal population, scenarios that used both methods—or used contraception exclusively—resulted in higher deviations from the target abundance (Fig. 4.7; Table C7). Use of contraception also resulted in higher variation around the target abundance than scenarios that only used lethal methods (Fig. 4.7; Table C8). Scenarios that used only lethal methods, or combinations of methods with low to moderate numbers of vaccines, typically had a coefficient of variations (CV) of population abundances of 0.05 or less once target abundance was reached. In contrast, scenarios that used large numbers of vaccines (>7,500 per year) had higher variation around the target abundance, and much higher negative deviations from that level (Fig. 4.7; Table C8).

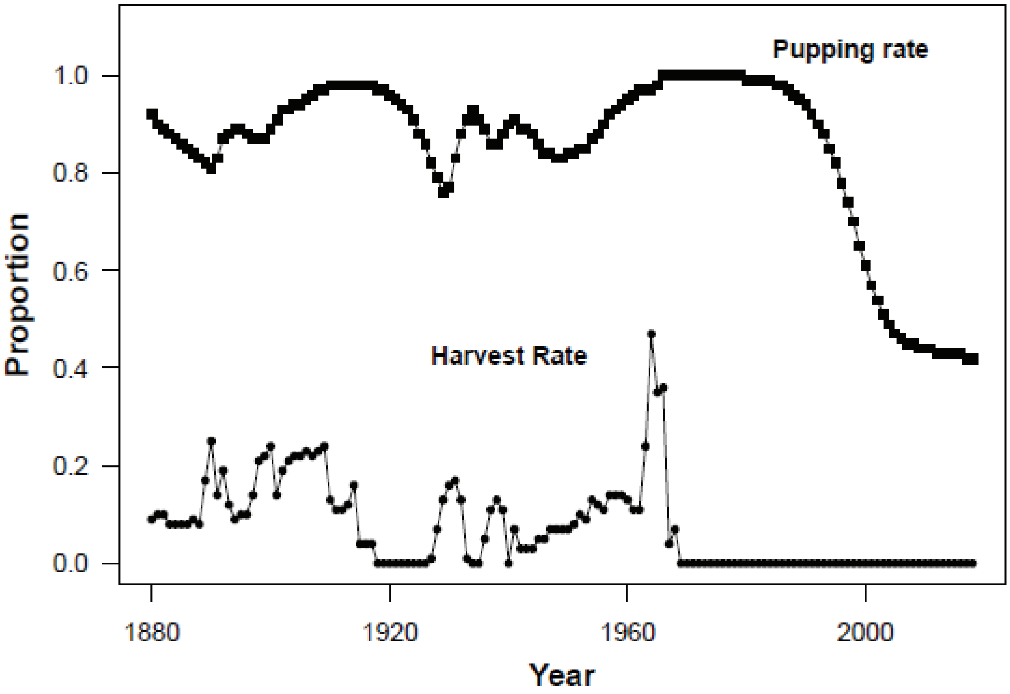

Figure 4.4: Estimated pupping rate (squares) in the population and harvest rates (circles) in the British Columbia harbour seal population between 1880 and 2018.

Generally, the base case and alternate age-structured models produced similar population responses across the various management scenarios simulated in this analysis (Fig. 4.7; Fig. 4.9). More specifically, for 13 of the 22 management scenarios (59%; Fig. 4.7) where target abundance was achieved, the median difference between the two models in terms of number of years to target abundance was only one year (Table C6). In all scenarios, the difference between the base and alternative age-structured models never exceeded four years. Because the base case version of the age-structured model estimated a higher current abundance of the harbour seal population, the time/effort needed to reach the target abundance was longer/higher compared to the alternate version (Fig. 4.7 and Fig. 4.9; Table C6). Compared with the age-structured models, the logistic model produced comparable outcomes in some scenarios, but markedly different outcomes in others (Fig. 4.7 and Fig. 4.9; Table C6). Specifically, when management scenarios involved lethal methods exclusively, the logistic population model projected dynamics that were very similar to the two age-structured models, particularly the base case (Fig. 4.7; Fig. 4.9). However, the logistic model failed to match the age-structured models in scenarios that relied exclusively, or heavily, on non-lethal methods. The clearest example of this discrepancy occurs in scenarios where non-lethal measures are used exclusively (e.g., row 1 of Fig. 4.7). Because the logistic model relies on adjustments to the intrinsic growth rate of the population (r) to simulate diminished fecundity, a population at or near carrying capacity will not decrease significantly as a result of simply decreasing r. While the logistic model did capture reduced fecundity from fertility control in scenarios where there was an initial depletion, that reduction was not as strong as the age-structured models (Fig. 4.9).

Finally, the change in population energetic requirements of a seal population reduced to target abundance by lethal measures (-47.3%) was not markedly different from the energetic requirements of one reduced by non-lethal measures (-53.2%) or a combination of the two (-46.2%) (Fig. 4.10). However, a population reduced by moderate to high levels of contraception is expected to have a smaller proportion of pups at the end of the 25-year management period (Fig. 4.10).

4.5 Discussion

Active population control of terrestrial and aquatic species has been used to recover their prey or competitors, to control invasive species, and to reduce conflicts with human populations. Providing decision-makers with multiple management options for altering abundance or reproductive capacity of these species is needed when logistical, ethical, and political considerations are present. Our analysis provides a quantitative assessment and comparison of lethal and non-lethal management actions that could potentially be used to manage British Columbia's harbour seal population, which may be impeding the recovery of salmon species of high conservation concern (Chasco et al. 2017b; Thomas et al. 2017).

Our simulation models suggest a considerable effort would be required to reduce the current harbour seal population to the 50% level proposed by some stakeholders, regardless of whether lethal or non-lethal measures are used. Using indiscriminate sustainable harvesting exclusively would require removing at least 6,000-7,000 adult animals each year to reduce the current population by half, within a 25-year period. Achieving the same reduction in population size within the same time period using fertility control would require sterilizing over 5,000 adult females annually. However, a combination of lethal and non-lethal methods could also be used effectively to deplete, then maintain the harbour seal population at the target abundance. This conclusion is consistent with the findings of similar studies that forecasted management options for terrestrial species (Raiho et al. 2015; Pepin et al. 2017). Management scenarios that include moderate to high levels of fertility control will have low precision relative to target abundance because of the delayed effect of sterilization on population fecundity—and will tend to deviate from the target abundance by a significantly higher magnitude than if lethal harvesting is undertaken.

4.5.1 Harbour seal population status in British Columbia

The “base case” age-structured population model we developed estimates the current (2018) abundance of British Columbia harbour seals is almost 100,000 animals (mean: 97,767; 95% PI: 87,553-107,982). This estimate is comparable to Olesiuk’s (2010) estimate of abundance for British Columbia in 2008 of 105,000 animals, as is our median estimate of population size around 1880 of between 55,000-60,000 animals. Further, the general population trends throughout the 19th and 20th centuries (and the levels of uncertainty) produced by our age-structured model are similar to the reconstruction in the same study, although our estimates of total abundance between 1930-1960 appear to be somewhat higher. Unlike previous work, our age-structured model was able to estimate current population demographics, and how they changed during periods of heavy harvesting and culling.

Our estimates imply a current sex ratio of nearly 60:40 females to males, and may be useful for updating bioenergetics models that estimate consumption and predation rates of harbour seal prey. For example, the most recent bioenergetics models for harbour seals in the region (Howard et al. 2013) uses sex and age proportions derived from studies conducted in the late-1960s, when the seal population was heavily exploited and well below carrying capacity (Bigg 1966, 1969). Our results suggest both the average age and the proportion of females in the population have increased since federal protection in the early-1970s (Fig. 4.2; Fig. 4.5). In addition to improving bioenergetics modeling efforts, updating estimates of population demographics could potentially reduce model uncertainty and/or inaccuracy. If lethal removals were to occur, this could be achieved through a sampling program similar to the one that occurred in the 1960s. Alternatively, tagging/marking studies (e.g., pup branding) could also be a viable method to update this information.

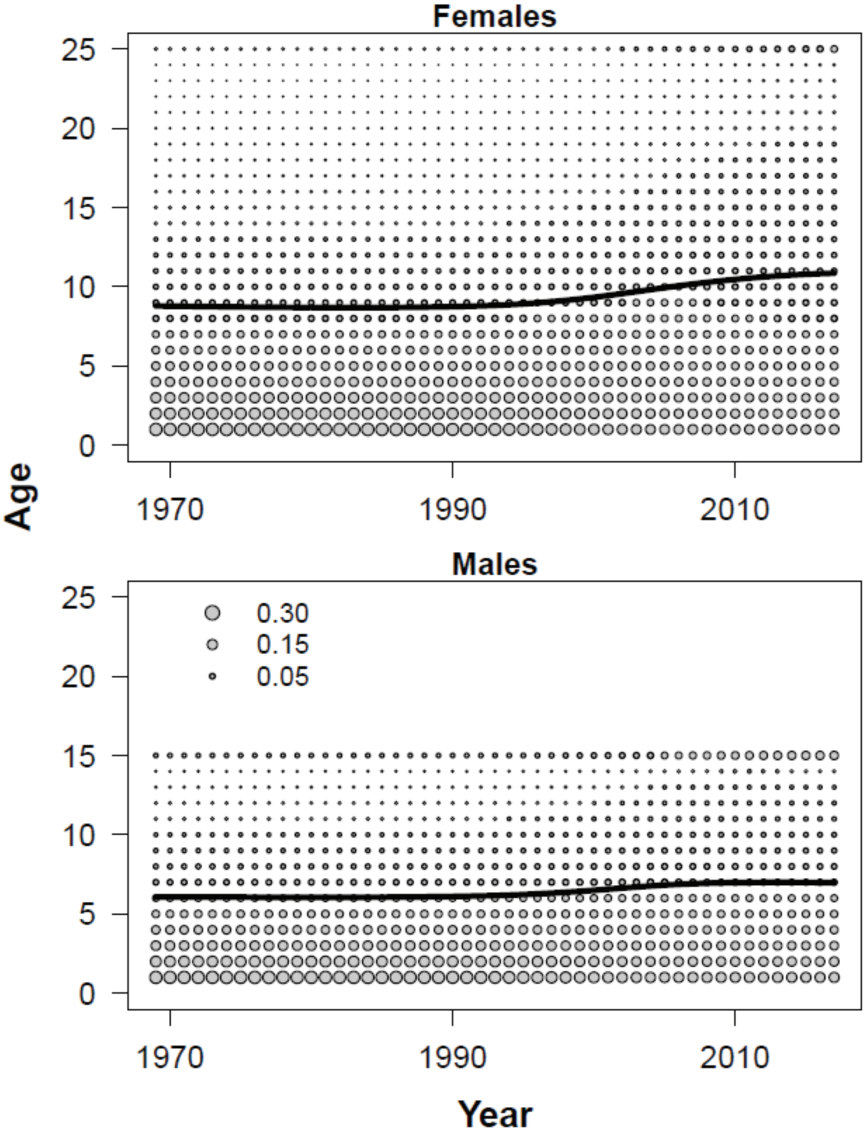

Figure 4.5: Bubble plots depicting proportions at age of British Columbia harbour seals between 1970 and 2018. Separate plots for females (top) and males (bottom) are shown. The radius of circles are proportional to the fraction of the population at each age (y-axis). The solid black line shows the mean age of the population in each year.

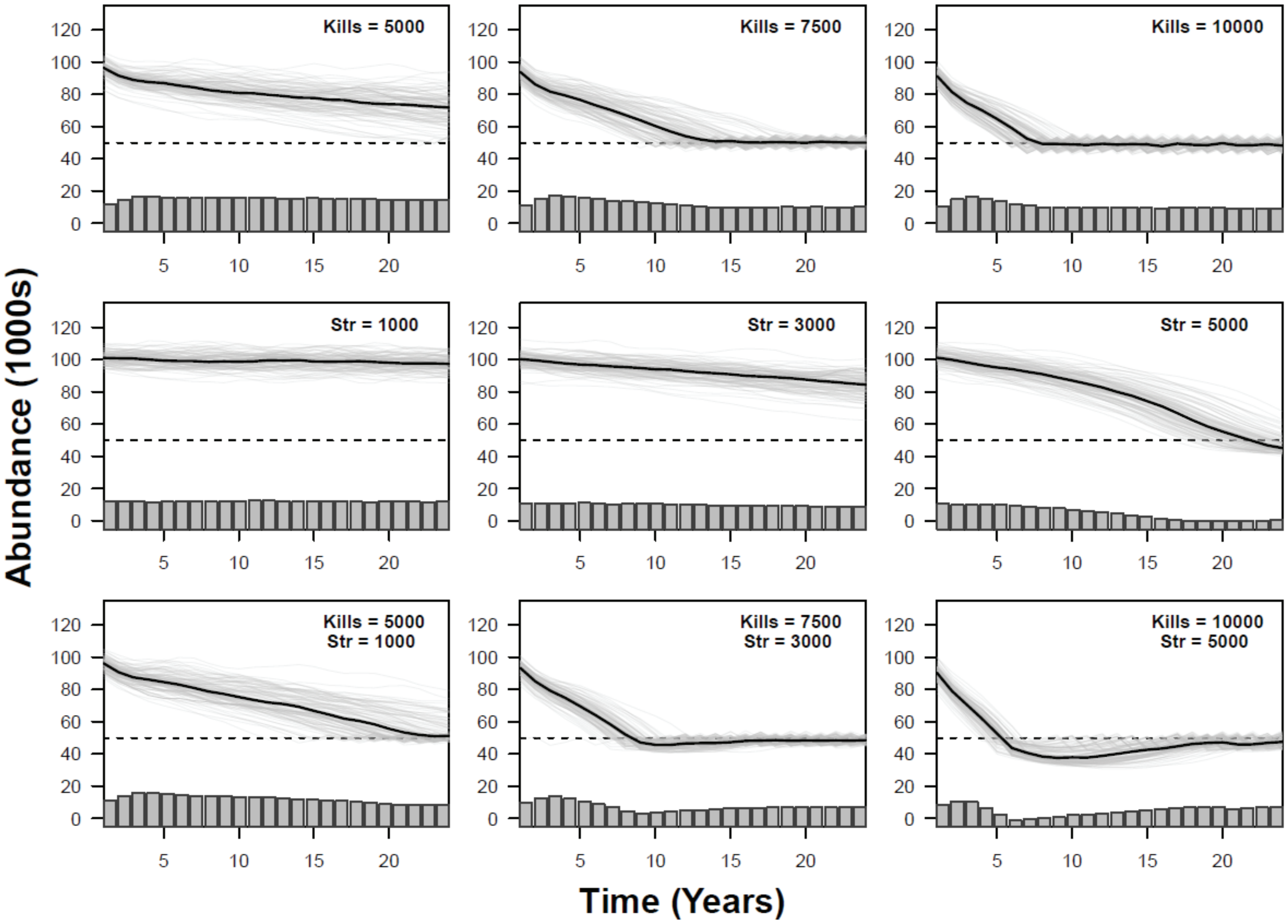

Figure 4.6: Projections of the British Columbia harbour seal population under multiple population control scenarios using indiscriminate lethal removals (Kills—number removed each year) and fertility control measures (Str—number of adult females sterilized each year), and combinations of both. For each scenario, 100 simulations of annual population abundance are shown (light gray lines), which were generated by combinations of parameters drawn from their posterior estimates. The solid black lines depict the median annual abundance (from 1,000 simulations), while the gray bars along the horizontal axis show the annual pup abundance. The horizontal dashed line shows the target abundance of 50,000 animals.

4.5.2 Differences among population models

In addition to the base case formulation, we also fit an alternate version of the age-structured model, as well as a logistic growth model to harbour seal abundance data. Evaluating multiple model formulations—which are, in essence, multiple hypotheses—is prudent in this situation, because different assumptions about the underlying process could significantly affect the results of our management simulation evaluation. In this case, we are also concerned about the sensitivity to and uncertainty around important population parameters, like carrying capacity, which may be important for the purpose of managing pinniped populations (Jeffries et al. 2003; Brown et al. 2005). Furthermore, some may prefer to apply the simpler logistic model to evaluate alternative population controls (e.g., PBPS 2019), assuming that the logistic model provides a close approximation of results obtainable from an age-and-sex structured model. We tested this assumption by evaluating lethal and non-lethal population control options, and found very different results were produced in some management scenarios.

While all three of the models we developed suggest that the British Columbia harbour seal population leveled off after its rapid increase from 1980-2000, there is some uncertainty around the current abundance relative to carrying capacity. The logistic model suggests a population carrying capacity of just below 100,000 animals, which would imply a current abundance that is very close, or at, its natural limit. However, both variants of the age-structured model suggest carrying capacity probably lies between 110,000-120,000 animals. We expect recent (and future) aerial surveys of seal numbers by DFO scientists will be important for reconciling the discrepancy between the estimates of the age-structured and logistic models.

We found that the logistic model could not properly evaluate the potential biological consequences of non-lethal population control options, and that it yielded markedly different predictions from those of the age-structured models (especially in management scenarios where non-lethal control methods were evaluated). For example, our lightly depleted logistic model failed to respond to vaccination (Figs. 4.7 and 4.9, Table C6) because vaccination affected only the surplus production term which was close to zero when abundance was close to carrying capacity (Appendix C). The logistic model also consistently underrepresented the population fluctuations that could be expected to occur after the target abundance was reached (Tables C7 and C8). If substantially overshooting the target abundance (e.g., deviations more than -20% of the target) is unacceptable, the logistic model would fail to reveal the policy options where this could occur (Table C7).

The median numbers of years to achieve target abundance were similar between the logistic and age and sex structured models for intensive lethal control options (e.g., when the number of seals culled per year was at least 10,000) (Table C6). However, the logistic model fell short in all other aspects. We therefore conclude that age- and sex-structured models are preferable for evaluating lethal and non-lethal population control options for harbour seals in British Columbia. Projection results obtained only from logistic-type models should be viewed with caution, especially when evaluating non-lethal controls and different combinations of lethal and non-lethal controls. The differences in projection results obtained between the different population dynamics models we considered indicates that it may be useful to evaluate the accuracy of the different models through a simulation study, or even a full management strategy evaluation (MSE) (Punt et al. 2020).

4.5.3 Active population control of harbour seals

Historical records of culls and bounties, combined with population abundance estimates from the early-1970s, show that the British Columbia harbour seal population was reduced to about 5% of its current population by lethal means (Bigg 1966, 1969; Olesiuk 2010). Thus, it is unsurprising that our simulation models predicted the seal population could be reduced by half in a relatively short time (< 10 years), if large numbers of animals (10,000 or more) were removed in consecutive years (Figs. 4.6-4.9). If indiscriminate harvesting were implemented at levels comparable to maximum efforts seen in the 20th century, a reduction of 50% of the population could be achieved in less than five years (Figs. 4.7-4.8).

Population prey requirements (in biomass) are proportional to population abundance, and would fall proportionally if the population was reduced, assuming that vulnerability to harvest was the same across all ages (Fig. 4.10). However, consumption does vary by sex and age. Thus, an extension of our analysis might be to use the age-structured model to assess how much consumption could be reduced depending on which age and size classes of seals are removed. The ability of the age-structured model to evaluate more nuanced alternatives like age-discriminate harvesting is another virtue of using population models with increased complexity.

We show that it may be possible to reduce the harbour seal population in British Columbia solely through fertility control. However, it would require a very large number of vaccines, and would probably take considerably longer to achieve a marked depletion of the population. Reducing the population by half within a 25-year management period would require at least 5,000 females to be vaccinated annually, for approximately 22-25 years. Vaccinating 10,000 females per year would achieve the same result in ~ 15 years. This difference in timing relative to numbers vaccinated highlights the non-linear relationship between the number of animals vaccinated and the time required to achieve the target abundance (Fig. 4.8).

Our projections further suggest that the target abundance could be maintained by vaccinations following a period of intense harvesting, but that it would still require an annual effort of around 5,000 vaccinations per year to prevent the population from slowly recovering. A combination of lethal and non-lethal actions performed simultaneously could also be used to achieve the target abundance and reduce the number of years to reach the management goal. For example, the target abundance could be reached in just 13-15 years by lethally removing 7,500 animals per year. Augmenting that policy with the vaccination of 1,000 adult females would reduce the time-to-target abundance to 8-9 years (Fig. 4.6). Such a policy might be advantageous if managers aimed to use only non-lethal management options in areas close to human population centers.

Both lethal and non-lethal methods of population control have potential risks and downsides that may be important for managers to consider. Regulated harvesting of pinnipeds (e.g., a First Nations hunt) would carry considerable political risk due to public concern for animal welfare (Yodzis 2001), and from skepticism within the scientific community regarding unintended consequences for the ecosystem (Lessard et al. 2005; Bowen and Lidgard 2013; Trites and Rosen 2019; Trzcinski 2020). However, an action involving lethal removals may also confer advantages in line with the goals of ecosystem-based fisheries management (Marshall et al. 2018b).

Because the direct effects of lethal control occur immediately, it is far easier to track performance metrics (e.g., change in abundance, current abundance) of a particular action from year-to-year. Because fertility control affects the reproductive rate of the population, there may be a delay, which could result in an inadvertent reduction of the population below the target level (Figs. 4.6, 4.7, 4.9). Similarly, if there were undesirable, unintended ecosystem impacts as a result of a reduction in the harbour seal population, a management action that uses lethal removals could be abandoned immediately, and recovery could commence beginning with the next cohort of pups (see: Fig. 4.9, column 1). In contrast, a reduction of the population achieved with fertility control could take decades to recover if a large fraction of females were already sterile, due to the longevity of female harbour seals (20-25 years). Short of lethally removing infertile animals, managers would be left with few options to recover the population. It is worth noting that annual monitoring of harbour seal abundance may not be feasible, due to limited resources. Thus, advantages of lethal measures may not be fully realized, should population monitoring only be conducted every three to five years, as has been the case in recent decades (Olesiuk 2010). Monitoring of other ecosystem indicators may also be necessary, in order to evaluate whether reducing the seal population is having a desired effect. This could potentially be very difficult to evaluate, as salmon populations can experience significant variation in survival and abundance from year to year, and these monitoring programs should be carefully considered prior to any reduction in the seal population.

One example of an indirect ecosystem impact that has concerned some scientists is the potential effect a reduced harbour seal population would have on mammal-eating transient killer whales, which are thought to be thriving in British Columbia due to an abundance of prey (Ford et al. 2013; Shields et al. 2018; Trites and Rosen 2019; Trzcinski 2020). Harbour seals are the preferred prey item of transient killer whales, so it is conceivable there could be negative consequences associated with a 50% reduction in the harbour seal population. However, previous research on killer whale foraging behavior suggests that these animals prefer to target pups and juvenile seals over full-grown adults (Baird and Dill 1995). Thus, it is possible that selective removals of older, mature individuals could mitigate impacts to killer whale prey availability, should a lethal management scenario be implemented. Such precision and selectivity would not be an option in a scenario that used only non-lethal measures, and our simulations suggest fertility control would reduce the proportion of pups significantly, relative to a population of the same size that was managed through harvesting (Fig. 4.6).

It can be safely assumed that controlling a wild pinniped population with lethal measures would be far less expensive than trapping, marking, and administering intramuscular injections to thousands of animals. One recent study evaluated the cost of implementing fertility control in a white-tailed deer (*Odocoileus virginianus*) population in North America and estimated the per animal cost of sterilization was over twice that of culling (Raiho et al. 2015). If the cost per animal of non-surgical contraception is assumed to be comparable to that of white-tailed deer ($750 USD), the annual cost associated with the vaccination of 5,000 harbour seals would be $3.75 million. In addition to the relatively expensive cost of contraception, there would likely also be high costs associated with the logistics, equipment and qualified personnel needed to execute a management action based on fertility control on a large-scale. Each animal would need to be captured, subdued, marked, and inoculated with a vaccine. Of course, estimating the true cost of lethal and non-lethal management options should also include possible profits from the sale of any meat or pelts from harvesting, as well as the costs of litigation that are almost certain to result from both approaches. Such calculations are outside the scope of our study, but would be important to consider prior to adopting any management action similar to those evaluated here.

4.5.4 Conclusions

Recovering predators and their prey in exploited marine ecosystems has proven to be a formidable challenge (Marshall et al. 2015; Samhouri et al. 2017). As such, effective conservation requires openly considering every available management option, even those that seem unconventional—along with a rigorous quantitative assessment of the trade-offs associated with each. Using simulation modeling, we showed that harbour seals in British Columbia could likely be managed effectively through lethal and non-lethal management actions, or a combination of both. Our projections suggest that lethal methods would be the most efficient, precise, and probably the least expensive way to reduce the population within a reasonable time horizon. However, if immuno-contraception with *zona pellucida* antigens is effective on harbour seals, fertility control may potentially control the population in British Columbia using a non-lethal management scenario alone, or in conjunction with lethal methods. Such an approach would likely be significantly more expensive than lethal removals, and would need further studies on captive populations to confirm the effectiveness of contraception on harbour seals.

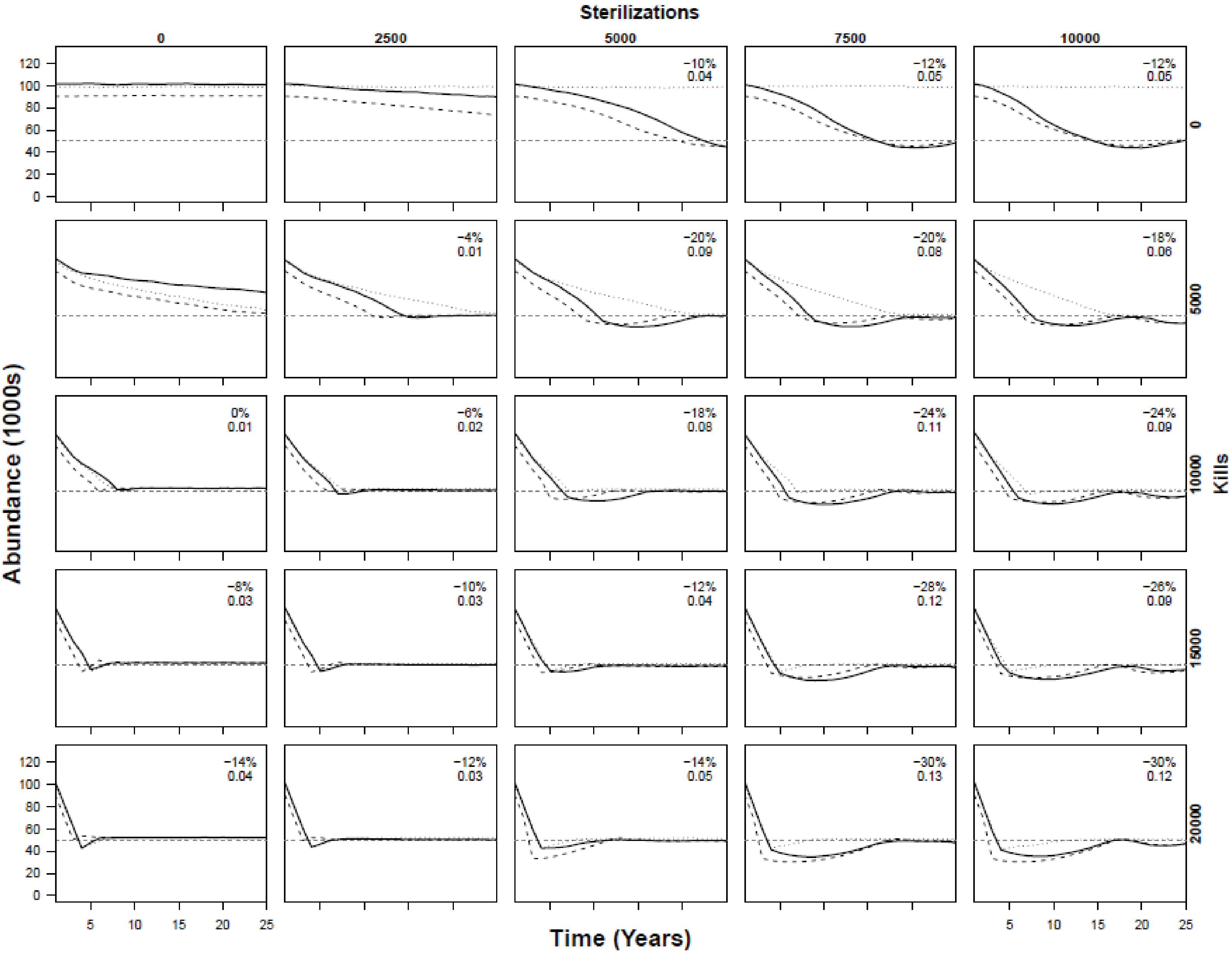
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Figure 4.7 (above): Projections of the British Columbia harbour seal population under multiple population control scenarios using combinations of both lethal and non-lethal (fertility control) measures. For each scenario, solid black lines depict the median annual abundance using the "base case" age-structured population model. Thick dashed lines show the projections using the alternate age-structured model (25% lower natural mortality rates). Dotted lines show the projections from the logistic growth model. 1,000 simulations were generated for each model. The thin horizontal dashed line shows the target abundance of 50,000 adult animals. Rows of the grid vary by the number of seals killed each year, while columns vary the annual number of adult females sterilized each year. Shown in the top right corner of each plot is the largest negative deviation (by percent) from the target abundance under the base case model, once the target has been achieved. Below this percentage is the coefficient of variation (CV) of the annual abundance under the base case model, once the target abundance has been achieved.

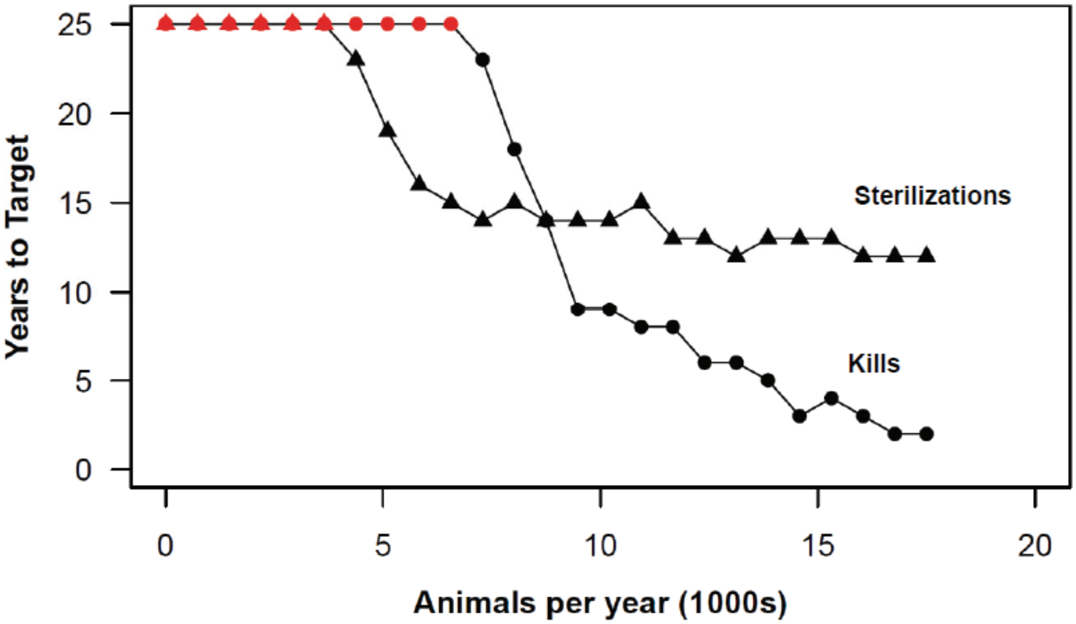
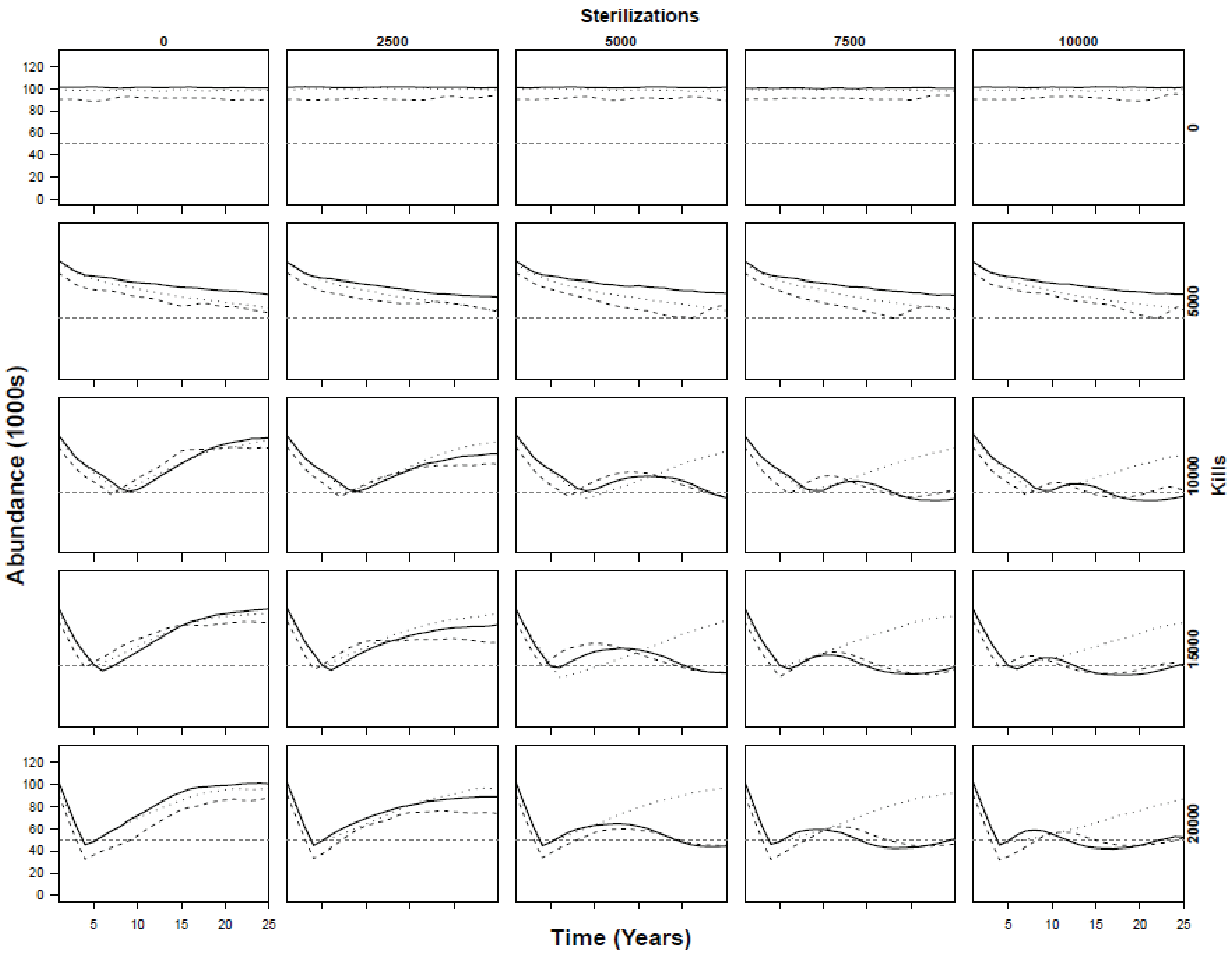


Figure 4.8: Median number of years to achieve the target abundance of 50,000 harbour seals in British Columbia, as a function of annual kills from indiscriminate lethal removals and annual sterilizations of adult females (triangles). Estimates of years to target abundance are based in 1,000 simulations for each management scenario, and assume uniform vulnerability across all age groups (including pups). Scenarios that achieved target abundance are shown in black, while those that never achieved the target abundance within 25 years are in red.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40
20
0
Time (Years)
5
10
15
20
25

Figure 4.9 (above): Projections of the British Columbia harbour seal population under multiple population control scenarios using combinations of both lethal and non-lethal (fertility control) measures. In contrast to Fig. 4.7, which depicts scenarios where both lethal and non-lethal methods are applied simultaneously from the beginning of the management period, scenarios shown here implement non-lethal methods only *after* target abundance has been reached through a period of harvesting. For each scenario, solid black lines depict the median annual abundance using the "base case" age-structured population model. Thick dashed lines show the projections using the alternate age-structured model (25% lower natural mortality rates). Dotted lines show the projections from the logistic growth model. 1,000 simulations were generated for each model. The thin horizontal dashed line shows the target abundance of 50,000 adult animals. Rows of the grid vary by the number of annual kills, while columns vary the annual number of sterilizations administered to adult females (sterile).

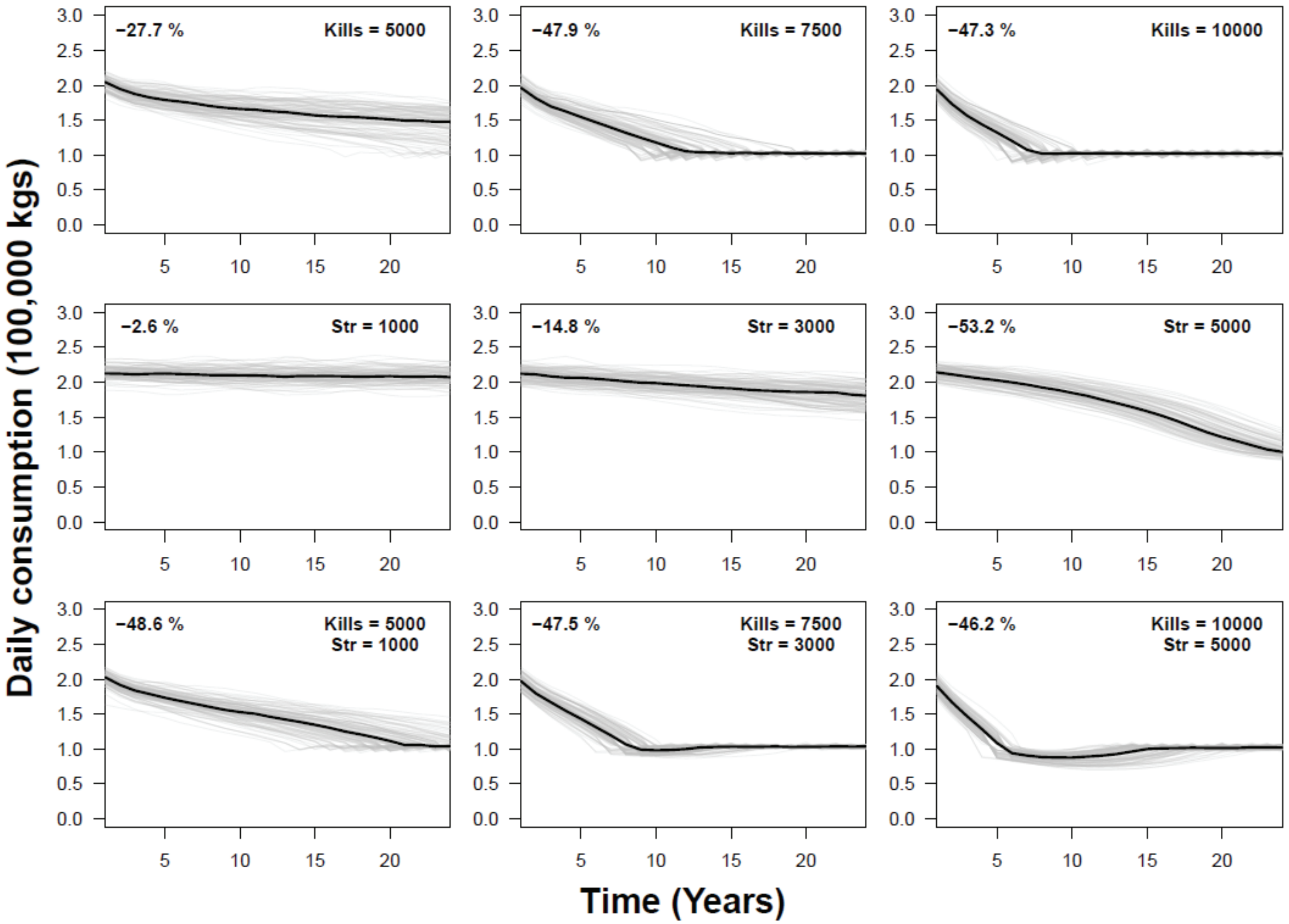

Figure 4.10: Projections of the total daily bioenergetics requirements for harbour seals in British Columbia under multiple population control scenarios using indiscriminate lethal removals (Kills) and sterilization (Str), and combinations of both. For each scenario, 100 simulations of daily population energetic requirements are shown (light gray lines), which were generated by combinations of parameters drawn from their posterior estimates. The solid black lines depict the median daily consumption (in kg) for the seal population. The median percent change in daily consumption over the 25-year management period is shown in the upper left corner of each plot, based on 1,000 simulations.

Chapter 5: Conclusions

My dissertation comprises three studies that aimed to advance current understanding of the role that harbour seal predation plays in the survival and productivity of Chinook and coho salmon populations in the Salish Sea, and the potential management alternatives that could be used to mitigate the effects of predation. In Chapter 2, I evaluated evidence for a relationship between harbour seal density and productivity of 20 wild Chinook salmon populations in the Salish Sea and Washington Coast. My third chapter combined harbour seal diet data and a model of predation on juvenile salmon, with the goal of estimating how many young fish are consumed by seals each year in the Strait of Georgia, and the extent to which predation-related mortality has increased over the past several decades. Finally, in Chapter 4, I developed a sex- and age-structured population model for harbour seals in British Columbia that was used in simulation modeling to evaluate lethal and non-lethal methods of reducing their abundance. This modeling framework may help inform managers who are considering actively managing the seal population to promote recovery of salmon populations.

5.1 Summary of research hypothesis and findings

5.1.1 Chapter 2

In Chapter 2, I evaluated the degree of statistical support for an association between harbour seal abundance and the productivity of wild Chinook salmon stocks in the Salish Sea ecosystem and Washington Coast. If seal predation is a major contributing factor to the declines in Chinook salmon in regions like the Salish Sea and Washington Coast, one might expect to find a strong negative correlation between some proxy of seal predation—such as abundance or density of animals—and the survival or productivity of Chinook salmon stocks. Furthermore, it is conceivable that if predation effects do exist, they may be similar among sub-populations of salmon within close proximity to one another.

This study was the first thorough correlative analysis of the relationship between the increases in harbour seal abundance and the coincident declines in abundance and marine survival of wild Chinook salmon stocks since the 1970s. I evaluated multiple Bayesian hierarchical models that were spatially explicit, and controlled for an alternative hypothesis that releases of hatchery Chinook salmon—which have also increased since the 1970s—may be negatively impacting wild populations. Then, I also used the parameter estimates from the best-performing model to infer the impact of seal predation on fisheries management reference points (e.g., maximum sustainable yield) for each Chinook salmon stock.

My analysis found that regional seal density had far more explanatory power than the abundance of hatchery-origin conspecifics, with regard to variation in wild Chinook salmon productivity. Specifically, 14 out of 20 Chinook salmon stocks in the Salish Sea and Washington Coast showed strong and statistically significant negative relationships with seal density, while none were strongly negatively associated with hatchery releases. This finding is similar to a recent study that used a comparable approach to assess the relationship between the aggregate marine survival rate of hatchery-origin Chinook salmon and harbour seal abundance in the Salish Sea (Sobocinski et al., *in review*). Interestingly, there was not strong support for significant regional differences in the effect size of seal density. Model coefficients implied an average decrease in maximum sustainable yield of 74% across all 20 Chinook salmon stocks, as a result of increases in seal abundance since the 1970s, while the effect of hatchery releases on management reference points stocks appeared to be neutral. This corroborates recent bioenergetics studies that revealed the possibility of high consumption rates of Chinook salmon by marine mammal predators in the Salish Sea (Chasco et al. 2017a, b).

Considering the objectives of this study, in addition to the existing body of research on interactions between marine mammals and salmon, my findings are important for three primary reasons. First, the analysis provides further evidence of a causal relationship between seal predation and declines in some Chinook salmon stocks in the northeastern Pacific. Second, that lack of evidence for negative impacts of hatchery releases on wild stocks should be of interest to managers that are currently considering increased hatchery production as a way to promote recovery of southern resident killer whales (Southern Resident Orca Task Force 2018; WDFW 2019). Finally, this work highlights the need for forecasting and assessment models used to manage Pacific salmon populations to consider accounting for the effects of marine mammal predation. Most current management models tend to focus on abiotic and environmental factors, but there is now ample evidence that biotic factors should also be included.

5.1.2 Chapter 3

The objective of Chapter 3 was to develop mathematical models that estimate how many juvenile Chinook and coho salmon are lost to harbour seal predation annually in the Strait of Georgia, British Columbia. The models I developed in this chapter expanded on recent research that used novel molecular techniques (i.e., DNA metabarcoding) to describe the diet of harbour seals in the Strait of Georgia (Thomas et al. 2014, 2017). Estimates of the proportions of juvenile Chinook and coho salmon in the seal diet were integrated into models that capture the total prey requirements of the seal population, in addition to the growth, mortality, and abundance of juvenile salmon. The models were fit to salmon abundance data from trawl surveys in the Strait of Georgia, which allowed me to estimate the numbers of individual salmon consumed by seals and infer the contribution of seal predation-related mortality relative to the total natural mortality experienced by salmon during their first year at sea. If the hypothesis that harbour seal predation is significantly impacting marine survival of juvenile salmon in the Salish Sea is valid, and the statistical relationships we identified in Chapter 2 are causal, I expected the models to predict relatively large numbers of juvenile Chinook and coho salmon being consumed by seals in the spring and summer.

I estimated that harbour seals consumed an average of 37-44% of juvenile Chinook salmon, and 46-59% of juvenile coho salmon annually, from 2004-2016. These calculations imply that mortality from harbour seal predation has increased rapidly since the 1970s for Chinook and coho salmon, if our assumptions about freshwater production are accurate. While the predation rates reported here are substantial, they are not necessarily unexpected, given the strong negative correlations between seal abundance and survival/productivity of both prey species (Chapter 2/Nelson et al. 2019b; Sobocinski et al., *in review*), in addition to the high estimates of consumption of Chinook salmon in other studies (Chasco et al. 2017a, b). An important secondary finding is the apparent spike in mortality from seal predation during the middle of the summer, after both Chinook and coho salmon have moved away from the river mouths they out-migrate from. This is noteworthy because it suggests that seals are not exclusively targeting smolts in estuaries shortly after marine entry, and that seal predation appears to be a prolonged threat to young salmon throughout the first several months in the marine environment. However, it appears that seal-related mortality is higher upon ocean entry for young coho salmon compared to Chinook salmon, as corroborated by a recent field study in the Strait of Georgia, which identified the same pattern (Allegue et al. 2020).

The results of this chapter are important contributions to our understanding of which factors drive marine survival of Chinook and coho salmon in the Salish Sea, and may also help identify effective management actions for reducing seal predation on young salmon. My findings provide further evidence of a causal relationship between seal predation and marine survival of Chinook, which has been suggested by previous studies (Chasco et al. 2017a, b), and also represent the first estimates of the annual number of juvenile coho salmon consumed by harbour seals in the region. These results should be considered in future efforts to manage and recover Chinook and coho salmon populations in the Strait of Georgia, as seal predation appears to be one plausible explanation for the rapid declines in marine survival since the 1970s. Finally, the seasonal mortality dynamics predicted by my models show that any management action that involves targeted culling of individual seals, i.e., "problem animals", in river mouths or estuaries should be met with skepticism. Because of sustained predation levels throughout the first several months at sea, such tactics are unlikely to yield any realized increase in survival and recruitment, particularly if seals are targeting larger individuals in the pelagic zone (Tollit et al. 1997; Nelson et al. 2019a).

5.1.3 Chapter 4

In Chapter 4, I used a simulation-based approach to evaluate the viability of two potential approaches to controlling the harbour seal population in British Columbia, and the tradeoffs associated with each. Should managers choose to embark on a policy that involves active management of the harbour seal population, simulation modeling can be used to provide coarse estimates of the time and effort needed to achieve certain goals, such as a reduction of the seal population to a target abundance. The two approaches I evaluated here were 1) lethal culling, which was used in the early- and mid-twentieth century to control harbour seal populations in

British Columbia, and 2) contraception of female animals through vaccine injections, which have shown some promise in pilot studies involving grey seals on the eastern coast of North America (Brown et al. 1997).

To develop a realistic simulation of interactions between the harbour seal population and the potential management scenarios, I needed to develop a population model capable of capturing the relevant characteristics of the seal population, such as total abundance and the intrinsic dynamics of mortality and growth. While a simple logistic growth model would likely suffice to test some management scenarios, I posited that a population model that explicitly accounts for the sex and age structure of the population could be useful within the context of a simulation-based approach to evaluating management alternatives. Accordingly, I developed a simple logistic growth model and a fully sex- and age-structured population model of the British Columbia harbour seal population, and compared the predictions of each under numerous management scenarios that included indiscriminate culling, sterilization, or combinations of both.

I found that both the logistic and age-structured models fit the seal abundance data well, although there were small differences in estimates of key population parameters like carrying capacity. The estimation of current abundance suggests that British Columbia's harbour seal population abundance is about 100,000 animals, which is in general agreement with previous studies (Olesiuk 2010). As expected, both models predicted that intense (>10,000 animals per year) indiscriminate culling would reduce the seal population rapidly, achieving the target abundance proposed by certain stakeholders of 50% within five years. Conversely, reduction of the seal population through contraception of large numbers of females would take much longer to achieve. Annual applications of even moderate to large numbers of vaccines would likely take a decade or two to accomplish a reduction of 50% of the current population. However, it is possible that lethal and non-lethal methods could be used in conjunction to achieve a 50% reduction of the population, within a reasonable time horizon (< 10 years). A general comparison of scenarios that used culling with those that used contraception showed that variation around target abundance was less for culling. In other words, adherence to target abundance was more difficult using contraception, which was due to the delayed effect of sterilization. Finally, based on previous case studies involving management of terrestrial species (e.g., white-tailed deer), and on the coarse estimates here, it is reasonable to assume that the cost (per animal) of managing the seal population through contraception would be considerably higher than culling.

5.2 Research limitations and future directions

In light of the findings reported in the preceding chapters of this dissertation, there are several limitations and topics that warrant consideration for future research. First, it is worth noting that throughout the development of my dissertation, multiple correlational studies (including Chapter 2 or Nelson et al. 2019b) have found associations between some measure of harbour seal abundance and survival (or productivity) of Chinook and coho salmon in the Salish Sea. One recent study did not account for spatial variation, and used an aggregate of stocks instead of accounting for stock-effects, but it did allow for non-linear relationships and accounted for a composite of abiotic and biotic covariates (Sobocinski et al., *in review*). Thus, I believe further correlational studies like these are probably of limited utility, given there is now strong correlational evidence for impacts of seal predation on Chinook and coho salmon. Taken together, these studies suggest predator abundances should be considered for inclusion in future forecasting and stock assessment modeling efforts.

With regard to my findings in Chapter 3, which involved estimating consumption of juvenile salmon by harbour seals, there are several issues that could be expanded upon in future research. While new DNA-based approaches for describing the harbour seals diet have been a marked improvement over traditional "hard parts" methods (Thomas et al. 2014, 2017)—i.e., their ability to identify prey to species level—one aspect of prey identification of salmonids in pinniped diets that seems worthy of investigation is the potential for genetic stock identification using DNA extracted from fecal samples. The ability to differentiate salmonid prey by origin (hatchery vs. natural) or by stock (population) would be beneficial for multiple reasons. For example, while marine survival of Chinook salmon stocks in the Salish Sea are generally depressed, there are exceptions (e.g., South Thompson River; Beamish et al. 2010a and Neville et al. 2015). Identifying disparate rates of seal predation among salmon stocks could reveal predation "hotspots", where certain populations are especially vulnerable to predation. Similarly, it may be useful to know whether wild- or hatchery-origin salmon are being consumed at higher rates, which could help design release strategies that minimize predation overall, or buffer wild stocks via predator swamping (Furey et al. 2016; Nelson et al. 2019a; Allegue et al. 2020).

The predation modeling framework I developed in Chapter 3 could potentially be applied to other salmon predators, as well. Some stakeholders and scientists have suggested that efforts to investigate other sources of predation should be made prior to any attempt to reduce the harbour seal population (Trites and Rosen 2019; Trzcinski 2020). DNA metabarcoding techniques have been used to quantify fish predation by avian species (Correia et al. 2019), and could be extended to other marine mammal and fish predators. "End-to-end" ecosystem modeling simulations of the Salish Sea are currently underway and my modeling approach could compliment or serve as inputs to these efforts.

An important limitation of our predation model is that it essentially treats the Strait of Georgia as a single discrete box that does not explicitly account for immigration or emigration of predators or prey. As discussed in Chapter 3, Chinook and coho salmon, and harbour seals probably move between the Strait of Georgia and Puget Sound in significant numbers (Rice et al. 2011; Peterson et al. 2012; Beacham et al. 2016). A more realistic predation model might treat the entire Salish Sea region as a single box, or as a composite of multiple regional boxes with animal movement among them. While Chasco et al. (2017b) recently developed such a framework for Chinook salmon in the Salish Sea (and the west coast), a next step could be to develop a similar analysis for coho salmon.

Similarly, a Salish Sea-wide population model for harbour seals could also be useful, not just as a potential extension of a predation model, but for evaluating management actions similar to those evaluated in Chapter 4 (S. Pearson, Washington Dept. of Fish and Wildlife, Olympia, WA, USA, pers. comm.). Extending the seal population model south to include animals residing in Puget Sound could facilitate trans-boundary efforts to monitor and manage the population, and would also allow for "borrowing" of information through shared data. One example of this may include updated demographic information, which has not been updated since data were collected in the 1960s (Bigg 1969).

While further data collection and model-building efforts could be conducted to provide further support for or against a causal relationship between seal predation and the decline of Chinook and coho salmon, they will not contribute to resolving whether the predation rates are additive, or if some degree of compensatory mortality would occur if seal predation was lowered through active population control (e.g., culling, contraception). Several studies have found evidence of compensatory mortality on juvenile salmonids involving avian predators (Tucker et al. 2016; Haeseker et al. 2020), but I am not aware of any studies that show similar dynamics involving marine mammal predators. All told, uncertainty in the salmon marine mortality schedule and the complexity of the Salish Sea marine food web are significant obstacles to extrapolating with uncertainty my estimates of juvenile salmon consumption into reductions in adult salmon abundance.

Finally, viewing the findings of this thesis within the broader context of salmon abundance in the north Pacific may provide insights into the role that pinniped predation ultimately plays in the failure of Chinook and coho salmon populations to recover following severe decreases in abundance in the 1970s and 1980s. It is important to note that while species like Chinook salmon have declined over the entire west coast of North America (Welch et al. 2020), abundances of other Pacific salmon species like pink and chum are at historic highs (Ruggerone and Irvine 2018). Sockeye salmon (*O. nerka*) populations have experienced highly variable returns in the southern part of their range in British Columbia and Washington State, but appear to be thriving in the northern part of their range, despite high abundances of competitors. Changes in climate may be mediating impacts of competition on sockeye production (Connors et al. 2020). Recent analyses suggest that climate change and competition may also negatively impact Chinook and coho salmon populations (Ruggerone and Goetz 2004; Manuta et al. 2015; Kendall et al. 2020).

Interestingly, juvenile sockeye salmon also appear in the harbour seal diet at levels similar to juvenile Chinook and coho salmon in the Salish Sea (Thomas et al. 2017), where pinniped predation could explain about 50% of the marked decrease in productivity and abundance of adult Fraser River sockeye since the 1990s (Walters et al. 2020). These findings, combined with evidence of broad, ocean-scale environmental drivers like climate change have prompted some to question whether pinniped predation is merely a proximate source of mortality for juvenile Chinook and coho salmon rather than the ultimate cause of declines in abundance and productivity since the 1970s. As has been the case with competition and density-dependence, it may be that other environmental and ecological factors mediate predation (Pink and Abrahams 2015; Wells et al. 2017). Future research and monitoring efforts should thus address these major knowledge gaps about the potential role of pinniped predation in salmon population dynamics, especially when developing new management alternatives.

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Appendices

Appendix A

A.1 Harbour seal abundance modeling

Aerial survey data from British Columbia and Washington was used to estimate harbour seal abundance for years missing from the time-series in published studies (Jeffries et al. 2003; Olesiuk 2010). To impute the abundance of seals in missing years, we employed a univariate state-space model that assumes density-dependence and accounts for process and observation error. As the population dynamics of seals on the Washington coast are likely different than the Salish Sea, separate models were developed to estimate annual abundances for three regions (Strait of Georgia, Puget Sound, and Washington coast).

Factors mediating population growth in seal populations are likely availability of prey and suitable haul-out habitat (Brown et al. 2005). The distribution/availability of seals' primary prey items in the estuarine habitats of the Salish Sea (herring, gadids, and adult salmon [see: Lance et al. 2012 and Howard et al. 2013]) is likely much different than coastal Washington (Steingass 2017). The different correction factors and survey protocols were applied to aerial survey methods (see below) in each region also justified the use of separate models for each region.

The approach integrates count data from multiple sub-regions to infer a common regional trend in population dynamics (see Jeffries et al. [2003] and Olesiuk [2010] for descriptions of these sub-regions). To estimate the regional annual abundance using count data from multiple sites within a region, we assume a single well-mixed population can be represented by the process model (Holmes et al. 2012):

(Eq. A1) $$x_t = bx_{t-1} + \mathrm{u} + \mathrm{w}_t$$

where x_t is natural log of the abundance of seals in year t, b dictates how fast the state reverts to the mean, u is the average population growth rate, and w_t is the deviation in year t. We assumed the deviations were normally distributed: $w_t \sim Normal(0, q)$, where q is the process variance.

We assumed the count data from each sub-region are observations of a common regional population trend. In other words, these sub-regions are not isolated from one another, and animals move and intersperse among them. This is supported by studies describing harbour seal movement patterns derived from tag data (Peterson et al. 2012). As such, the observation model is

(Eq. A2) $$\mathbf{y}_t = x_t + \mathbf{a} + \mathbf{v_t}$$

where $\mathbf{y}_t$ are the abundance time-series for the sub-regions, $\boldsymbol{a}$ is a vector of scalars that capture the bias between the counts and the total population, and $\mathbf{v_t}$ is a vector of observation error variances, which we assume are the same in each region because they were performed with the same aerial survey protocols. We assumed the observation error on the natural log of the counts was normally distributed. For the surveys in Washington State a correction factor of 1.53 (Huber et al. 2001; Chasco et al. 2017a) was used to expand abundance estimates, while Strait of Georgia survey data was corrected using site-specific multipliers presented in DFO's published reports (Olesiuk 2010). The model described above was fit to the aerial survey data with maximum likelihood using the MARSS package in R (Holmes et al. 2012).

A.2 Estimation of management reference points (U_{MSY} and MSY)

Using equilibrium yield calculations (Walters and Martell 2004), we estimated two reference points for each population of Chinook salmon—the harvest rate that produces maximum sustained yield (U_{MSY}) and maximum sustainable yield (MSY)—over different combinations of independent variables to quantify the impact seal density and hatchery abundance have on yield. For each stock, we started with an initial spawning population, then used the estimated parameters from the best performing model (Model 1) to simulate cohorts of recruits. We then subjected the cohort to a natural mortality and maturity schedule, as well as a fishery. This process was repeated until the population achieved equilibrium. Yields were calculated across a range of exploitation rates (0.0-1.0, by increments of 0.01), over different combinations of seal densities and hatchery abundances, and the reference points associated with each combination were identified.

This iterative scheme was initialized by generating an estimate of the number of spawners at equilibrium: $S_{Equil,1} = 0.5\left(\frac{\alpha}{\beta}\right)$ (e.g. Korman et al. 1995). Then, the following age-structured population model was repeated until S_{Equil} had stabilized:

(Eq. A3) $$S_{Equil,i+1} = 0.5S_{Equil,i} + 0.5S_i$$

Where S_i is the number of spawners generated from $S_{Equil,i}$ at iteration i. The number of age-2 recruits (pre-fishery) in each iteration was generated from the generalized Ricker equation (Eq. 2.5) with parameter estimates from the best model in the analysis (Model 1):

(Eq. A4) $$R_{2,i} = S_{Equil,i}e^{(\alpha-\beta S_i+qSeal+hHatch)}$$

Recruits were then subjected to natural mortality prior to fishing. For each year in iteration i, recruitment at age was calculated by subtracting fish lost to harvest, natural mortality, and maturity:

(Eq. A5)
$$R_{a,i} = \begin{cases} R_{a-1,i}s_a & a = 3 \\ \left(R_{a-1,i} - C_{a-1,i} - S_{a-1,i}\right)s_a & a > 3 \end{cases}$$

where s_a is the age-specific natural mortality rate. We used the following natural mortality rates at each age: 40% for age-2, 30% for age-3, 20% for age-4, and 10% for age-5 (Sharma et al. 2013; PSC 2015). Catch at age is calculated by multiplying the recruits at age a by the harvest rate U:

(Eq. A6)
$$C_{a,i} = U \times R_{a,i}$$

The number of spawners at age a in iteration i is the product of post-fishery recruits and the proportion of fish that mature at a given age (p_a):

(Eq. A7)
$$S_{a,i} = \left(R_{a,i} - C_{a,i}\right)p_a$$

We assumed the following maturity schedule: 10% of fish have matured by age-3, 80% by age-4, and 100% by age-5 (PSC 2015). Finally, once the calculation from the above population model stabilized (usually between 20-40 cycles), we calculated the MSY and the harvest rate that produced MSY (U_{MSY}) for that combination of variables (seal density, hatchery abundance).

A.3 MCMC convergence

Visual inspection of trace plots showed all MCMC chains were sufficiently well-mixed, suggesting the chains had successfully converged. Additionally, the Gelman-Rubin diagnostic statistics (R-hat) for all parameters and quantities of interest did not exceed 1.00 in any of the candidate models used in the analysis.

A.4 Posterior predictive checking

Fig. 2.7 displays the posterior predictive intervals (95%) for Model 1 and the observed data for each of the 20 Chinook populations included in our analysis. The proportion of data points captured by the posterior predictive interval was 1.00 for 11 of the 20 stocks, and no less than 0.96 (Chilliwack, Nisqually, Quillayute) for the others. Of the 525 data points used in the analysis, the posterior predictive intervals of Model 1 captured 516 of them (98.3%). The Bayesian p-value for Model 1 was 0.66, which suggests the model is not inconsistent with the observed data (Fig. A1). There were no systematic differences apparent when visually comparing the replicated data (via the predictive distribution) to the observed data.

Table A1: Variance Inflation Factors (VIF) for each independent variable (seal density, spawners, hatchery [releases]) for each of the 20 stocks of Chinook salmon included in the study. The stock number in the first column corresponds to population information in Table 2.1. Summary statistics for each variable's VIF across all populations are included in the bottom rows of the table, and the number of data points (brood years) for each Chinook population dataset is shown in the last column (n). The mean VIFs were weighted by the size of the dataset (n).

Stock	Seal Density	Spawners	Hatchery	n
1	1.03	1.03	1.00	23
2	4.27	1.44	3.49	33
3	1.81	1.26	2.15	19
4	2.66	1.57	2.92	31
5	3.82	1.25	3.48	36
6	1.10	1.04	1.09	24
7	1.34	1.45	1.15	25
8	2.63	1.93	1.62	28
9	1.06	1.02	1.06	29
10	2.16	1.23	2.22	26
11	1.97	1.29	2.35	27
12	1.89	1.06	1.87	23
13	1.17	1.08	1.15	31
14	1.15	1.07	1.11	31
15	1.50	1.17	1.67	28
16	1.32	1.09	1.38	20
17	1.91	2.79	2.98	7
18	1.23	1.28	1.54	29
19	1.26	1.34	1.56	26
20	1.24	1.07	1.26	29
Min	1.03	1.02	1.00	7
Max	4.27	2.79	3.49	36
Mean	1.83	1.32	1.85	26.25
SD	0.91	0.41	0.81	6.19
Weighted mean	1.89	1.27	1.86	-

Table A2: Pearson correlation coefficients for three parameter combinations for 20 stocks of Chinook salmon, using the best performing model (Model 1). The stock number in the first column corresponds to population information in Table 2.1.

Stock	q, Ricker β	q, h	h, Ricker β
1	-0.09	-0.01	0.00
2	-0.21	-0.30	-0.07
3	0.00	-0.43	0.31
4	-0.27	-0.35	-0.22
5	-0.11	-0.62	-0.17
6	0.09	-0.13	-0.19
7	-0.57	0.03	-0.28
8	-0.41	-0.12	-0.07
9	-0.04	-0.22	-0.17
10	0.20	0.40	0.18
11	0.06	0.33	0.09
12	0.28	0.37	0.13
13	-0.26	0.16	-0.28
14	0.02	0.03	-0.01
15	-0.03	0.11	0.15
16	0.13	0.08	-0.20
17	0.38	0.04	-0.26
18	-0.05	-0.31	-0.37
19	0.06	-0.30	-0.34
20	-0.14	-0.32	-0.16

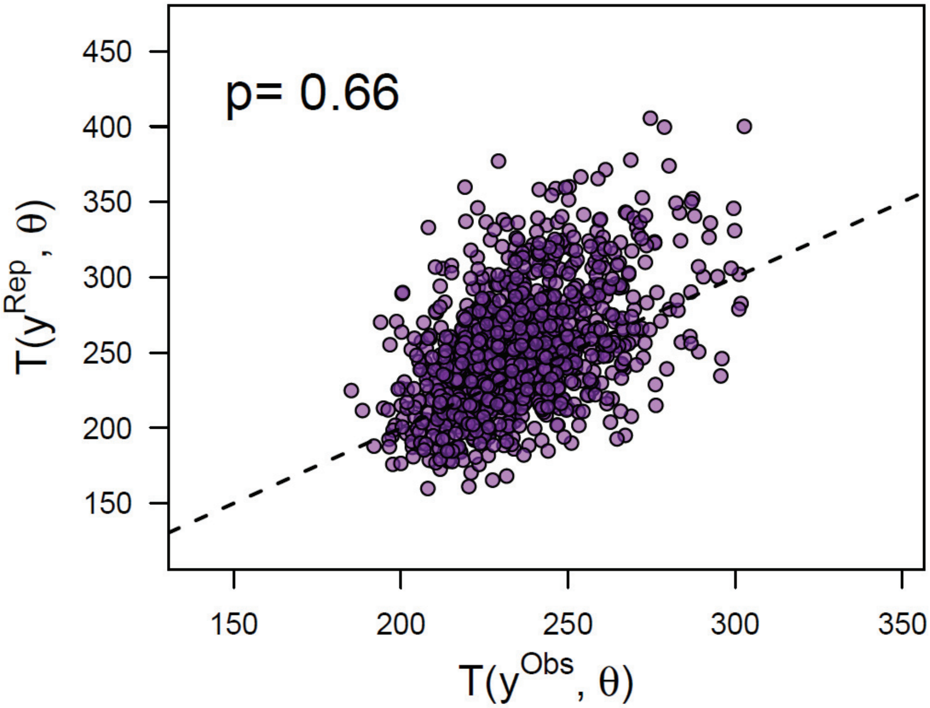


Figure A1: The relationship between 1,000 simulated (y-axis) and realized (x-axis) chi-squared discrepancy measures (T), which were used to calculate the posterior predictive p-value for Model 1. The dashed line depicts x = y. The Bayesian p-value of 0.66 suggests Model 1 provides a relatively good fit to the data.

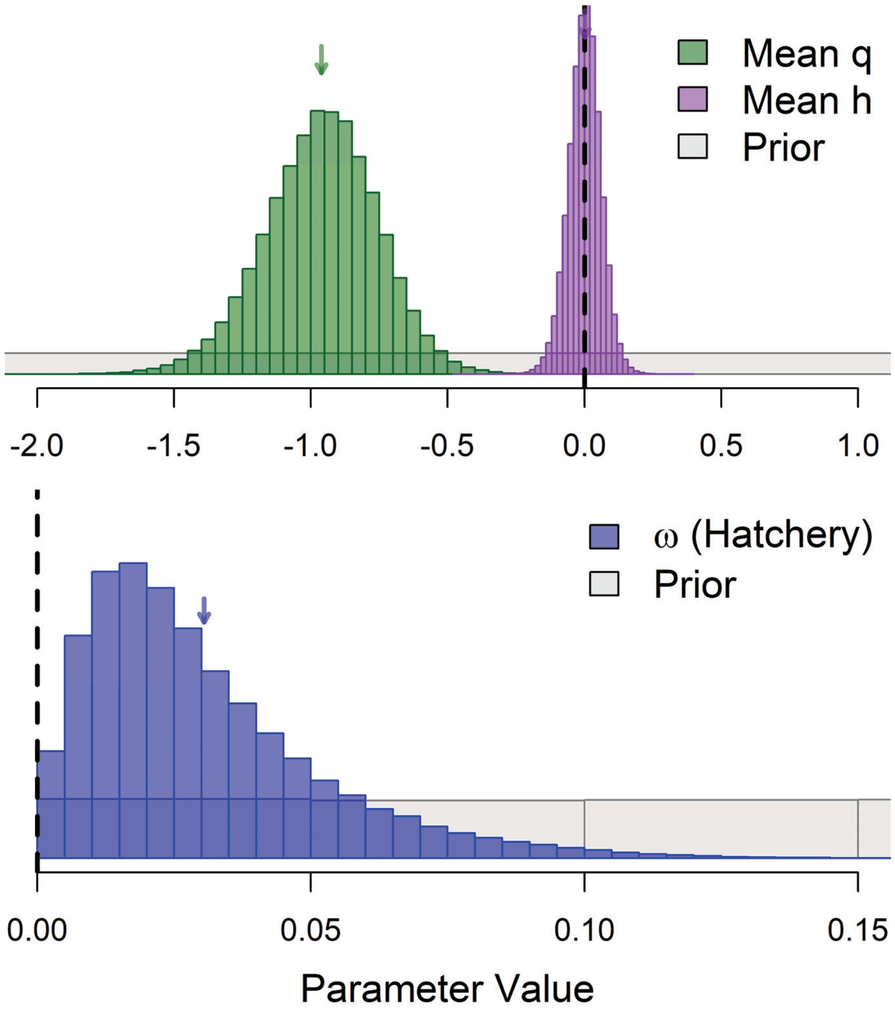
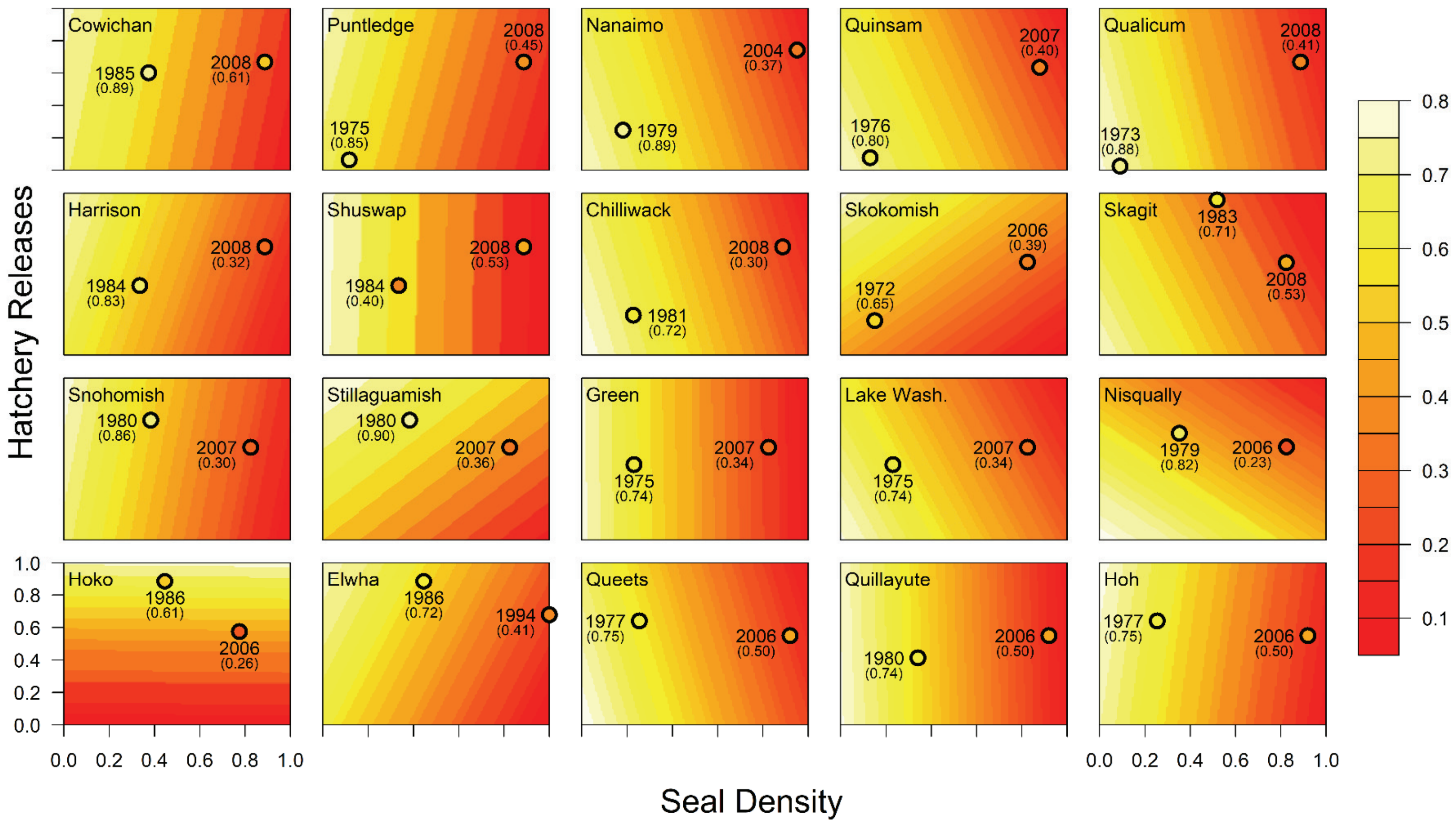


Figure A2: Histograms of the marginal posterior and prior distributions for harbour seal predation (q), hatchery production (h), and spatial relatedness (hatchery) (ω_h) parameters in stock-recruit models for 20 Chinook salmon populations. The top plot depicts the global means for q_i and mean h_i from Model 1. The lower plot shows the ω_h parameter of the CAR prior imposed on h_i in Model 2, which quantifies the degree of spatial relatedness among individual h_i parameters. Small arrows denote the mean value of the posterior distributions.



Hatchery Releases
Seal Density
Cowichan
1985 (0.89)
2008 (0.61)
Puntledge
1975 (0.85)
2008 (0.45)
Nanaimo
1979 (0.89)
2004 (0.37)
Quinsam
1976 (0.80)
2007 (0.40)
Qualicum
1973 (0.88)
2008 (0.41)
Harrison
1984 (0.83)
2008 (0.32)
Shuswap
1984 (0.40)
2008 (0.53)
Chilliwack
1981 (0.72)
2008 (0.30)
Skokomish
1972 (0.65)
2006 (0.39)
Skagit
1983 (0.71)
2008 (0.53)
Snohomish
1980 (0.86)
2007 (0.30)
Stillaguamish
1980 (0.90)
2007 (0.36)
Green
1975 (0.74)
2007 (0.34)
Lake Wash.
1975 (0.74)
2007 (0.34)
Nisqually
1979 (0.82)
2006 (0.23)
Hoko
1986 (0.61)
2006 (0.26)
Elwha
1986 (0.72)
1994 (0.41)
Queets
1977 (0.75)
2006 (0.50)
Quillayute
1980 (0.74)
2006 (0.50)
Hoh
1977 (0.75)
2006 (0.50)
1.0
0.8
0.6
0.4
0.2
0.0
0.0
0.2
0.4
0.6
0.8
1.0
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1

Figure A3 (above): Estimated harvest rate at maximum sustainable yield (U_{MSY}) over different combinations of seal density and hatchery abundance for 20 Chinook salmon stocks. Both seal density and hatchery abundance are standardized by the maximum value of each variable between 1970 and 2010. The observed combination of variables in the first and last brood year in the dataset for each stock are plotted (colored circles), along with the observed harvest rate (from PSC 2015a, b) for those years in parentheses.

Appendix B

Table B1: Ranges of parameter values used to formulate "prior" distributions for seal-related instantaneous mortality on Chinook and coho salmon in the Strait of Georgia.

		Coho		***Chinook***	
Parameter	**Description**	**Min**	**Max**	**Min**	**Max**
$N_s^{Natural}$	Initial abundance of natural-origin smolts (millions)	8.00	15.00	35.00	60.00
E_s'	Number of prey consumed by seals (millions)	4.00	8.00	10.00	15.00
M_s^{Fresh}	Freshwater/downstream mortality	0.22	0.69	0.36	1.00
M_s^{Winter}	Over-winter mortality	0.20	0.50	0.20	0.50
M_s^{Total}	Total mortality (first year)	3.00	4.00	4.00	5.00

Table B2: AICc values for predation models across multiple values of c_s.

	c_s				
Model	**0.80**	**0.90**	**1.00**	**1.10**	**1.20**
Chinook	NA	-1.86	-2.27	-1.83	-1.82
Coho	-1.49	-1.49	-1.49	-1.38	-1.39

Table B3: Mean annual harbour seal abundance in the Strait of Georgia, and annual total hatchery releases of Chinook and coho salmon from Strait of Georgia tributaries. Also shown is estimated wild production for both species from Strait of Georgia tributaries. Seal abundances were estimated using a state-space model fit to aerial survey data in Nelson et al. 2019b. Annual hatchery releases were collated using data from the RMIS database (www.rmpc.org; accessed June 2019).

		Chinook		*Coho*	
Year	**Seals**	**Hatchery**	**Wild**	**Hatchery**	**Wild**
2004	41,696	22.1	25.4	9.3	7.4
2005	40,625	19.9	25.4	9.1	7.4
2006	39,582	19.3	25.4	8.2	7.4
2007	38,565	19.1	25.4	6.5	7.4
2008	37,552	16.9	25.4	6.6	7.4
2009	37,915	17.8	25.4	7.6	7.4
2010	38,258	17.2	25.4	7.9	7.4
2011	38,605	15.4	25.4	9.0	7.4
2012	38,955	17.2	25.4	9.6	7.4
2013	39,308	13.9	25.4	7.4	7.4
2014	39,631	11.1	25.4	6.6	7.4
2015	39,631	13.7	25.4	6.5	7.4
2016	39,631	13.5	25.4	5.5	7.4

Table B4: Estimated annual seal-related instantaneous mortality rates and proportion of juvenile Chinook and coho salmon eaten during the first year at sea from 1970-2016. Estimates are extended from Tables 3.4 and 3.5. Shown are the median estimates for each year, and the 95% predictive intervals.

	Chinook		*Coho*	
Year	**Seal Mort.**	**Prop. eaten**	**Seal Mort.**	**Prop. eaten**
1970	0.08 (0.05-0.11)	0.04 (0.03-0.05)	0.10 (0.08-0.13)	0.07 (0.06-0.08)
1971	0.08 (0.06-0.12)	0.04 (0.04-0.05)	0.11 (0.08-0.14)	0.07 (0.06-0.08)
1972	0.08 (0.06-0.12)	0.04 (0.04-0.05)	0.11 (0.08-0.15)	0.07 (0.06-0.09)
1973	0.09 (0.06-0.13)	0.05 (0.04-0.05)	0.11 (0.09-0.15)	0.08 (0.07-0.09)
1974	0.10 (0.07-0.15)	0.05 (0.04-0.06)	0.13 (0.10-0.17)	0.08 (0.07-0.10)
1975	0.11 (0.08-0.17)	0.06 (0.05-0.07)	0.14 (0.10-0.19)	0.09 (0.08-0.11)
1976	0.13 (0.09-0.18)	0.06 (0.05-0.07)	0.16 (0.12-0.21)	0.11 (0.09-0.12)
1977	0.14 (0.10-0.21)	0.07 (0.06-0.08)	0.17 (0.13-0.23)	0.11 (0.09-0.13)
1978	0.15 (0.11-0.23)	0.08 (0.07-0.09)	0.19 (0.14-0.25)	0.12 (0.10-0.14)
1979	0.17 (0.12-0.26)	0.09 (0.07-0.10)	0.21 (0.16-0.28)	0.13 (0.12-0.15)
1980	0.19 (0.13-0.28)	0.09 (0.08-0.11)	0.23 (0.18-0.32)	0.15 (0.13-0.17)
1981	0.20 (0.14-0.31)	0.10 (0.09-0.11)	0.21 (0.16-0.29)	0.13 (0.11-0.15)
1982	0.23 (0.16-0.36)	0.11 (0.10-0.13)	0.26 (0.20-0.36)	0.16 (0.14-0.19)
1983	0.26 (0.17-0.39)	0.12 (0.10-0.14)	0.23 (0.17-0.31)	0.15 (0.12-0.17)
1984	0.30 (0.20-0.46)	0.14 (0.12-0.16)	0.25 (0.19-0.34)	0.16 (0.13-0.18)
1985	0.32 (0.22-0.51)	0.15 (0.13-0.17)	0.22 (0.17-0.30)	0.14 (0.12-0.16)
1986	0.33 (0.22-0.52)	0.15 (0.13-0.18)	0.23 (0.17-0.32)	0.15 (0.12-0.17)
1987	0.37 (0.25-0.59)	0.17 (0.14-0.19)	0.34 (0.25-0.47)	0.20 (0.17-0.23)
1988	0.39 (0.26-0.63)	0.17 (0.15-0.20)	0.38 (0.28-0.54)	0.22 (0.19-0.26)
1989	0.47 (0.31-0.78)	0.20 (0.17-0.24)	0.50 (0.36-0.72)	0.28 (0.23-0.32)
1990	0.59 (0.38-1.04)	0.24 (0.21-0.28)	0.60 (0.43-0.91)	0.32 (0.27-0.37)
1991	0.54 (0.35-0.91)	0.23 (0.19-0.26)	0.54 (0.39-0.78)	0.30 (0.25-0.34)
1992	0.56 (0.36-0.94)	0.23 (0.20-0.27)	0.52 (0.38-0.76)	0.29 (0.25-0.33)

1993	0.78 (0.49-1.48)	0.29 (0.25-0.34)	0.77 (0.54-1.22)	0.38 (0.33-0.44)
1994	1.20 (0.69-5.62)	0.38 (0.32-0.44)	1.16 (0.75-2.31)	0.49 (0.42-0.56)
1995	1.17 (0.70-5.21)	0.37 (0.32-0.43)	1.04 (0.72-1.90)	0.46 (0.39-0.53)
1996	1.29 (0.73-9.00)	0.39 (0.34-0.46)	1.11 (0.72-2.08)	0.47 (0.40-0.55)
1997	0.92 (0.57-2.14)	0.33 (0.28-0.38)	0.87 (0.60-1.44)	0.41 (0.35-0.48)
1998	0.84 (0.52-1.74)	0.31 (0.27-0.35)	0.76 (0.53-1.21)	0.38 (0.33-0.43)
1999	0.92 (0.57-2.03)	0.33 (0.28-0.38)	0.94 (0.64-1.59)	0.43 (0.37-0.50)
2000	1.20 (0.69-6.38)	0.38 (0.32-0.44)	1.01 (0.68-1.85)	0.45 (0.39-0.53)
2001	1.25 (0.71-5.59)	0.39 (0.33-0.44)	1.00 (0.68-1.62)	0.45 (0.38-0.51)
2002	1.16 (0.66-3.61)	0.37 (0.32-0.43)	1.02 (0.66-1.70)	0.45 (0.38-0.52)
2003	1.30 (0.74-6.11)	0.39 (0.34-0.45)	1.12 (0.73-2.09)	0.48 (0.41-0.55)
2004	1.25 (0.72-6.87)	0.39 (0.33-0.45)	1.25 (0.80-2.66)	0.51 (0.43-0.58)
2005	1.27 (0.72-6.30)	0.39 (0.33-0.45)	1.21 (0.78-2.67)	0.50 (0.42-0.57)
2006	1.22 (0.70-6.46)	0.38 (0.33-0.44)	1.24 (0.81-2.59)	0.51 (0.43-0.58)
2007	1.17 (0.69-4.09)	0.37 (0.32-0.43)	1.44 (0.91-5.11)	0.54 (0.46-0.63)
2008	1.20 (0.67-5.15)	0.38 (0.32-0.43)	1.37 (0.85-3.29)	0.53 (0.45-0.60)
2009	1.17 (0.68-6.13)	0.38 (0.32-0.44)	1.22 (0.80-2.72)	0.50 (0.43-0.58)
2010	1.21 (0.69-6.79)	0.38 (0.33-0.44)	1.21 (0.78-2.47)	0.50 (0.43-0.57)
2011	1.30 (0.75-7.00)	0.40 (0.34-0.46)	1.12 (0.75-2.12)	0.48 (0.41-0.55)
2012	1.25 (0.71-6.53)	0.39 (0.33-0.44)	1.06 (0.71-1.95)	0.46 (0.40-0.53)
2013	1.43 (0.75-7.67)	0.41 (0.35-0.48)	1.36 (0.82-3.30)	0.52 (0.45-0.61)
2014	1.59 (0.84-7.68)	0.43 (0.37-0.50)	1.52 (0.92-6.27)	0.56 (0.47-0.63)
2015	1.46 (0.81-6.76)	0.42 (0.35-0.48)	1.54 (0.96-7.56)	0.56 (0.48-0.64)
2016	1.47 (0.81-8.00)	0.42 (0.35-0.48)	1.78 (1.05-8.00)	0.59 (0.50-0.68)

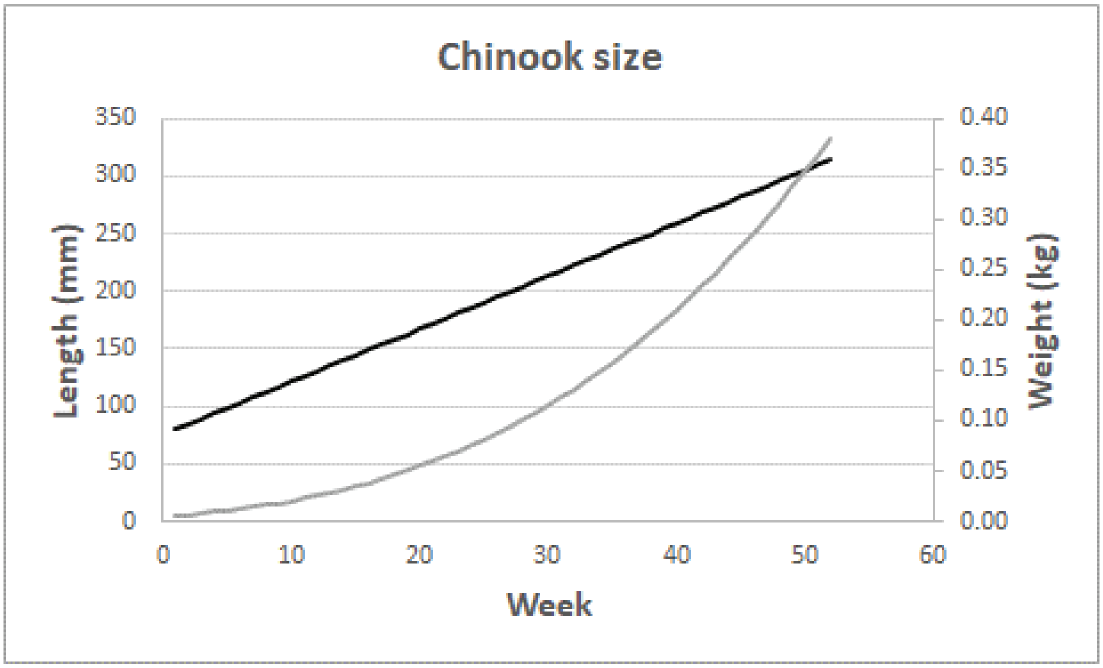


Figure B1: Juvenile Chinook salmon length (black) and weight (gray) over time for the harbour seal predation model.

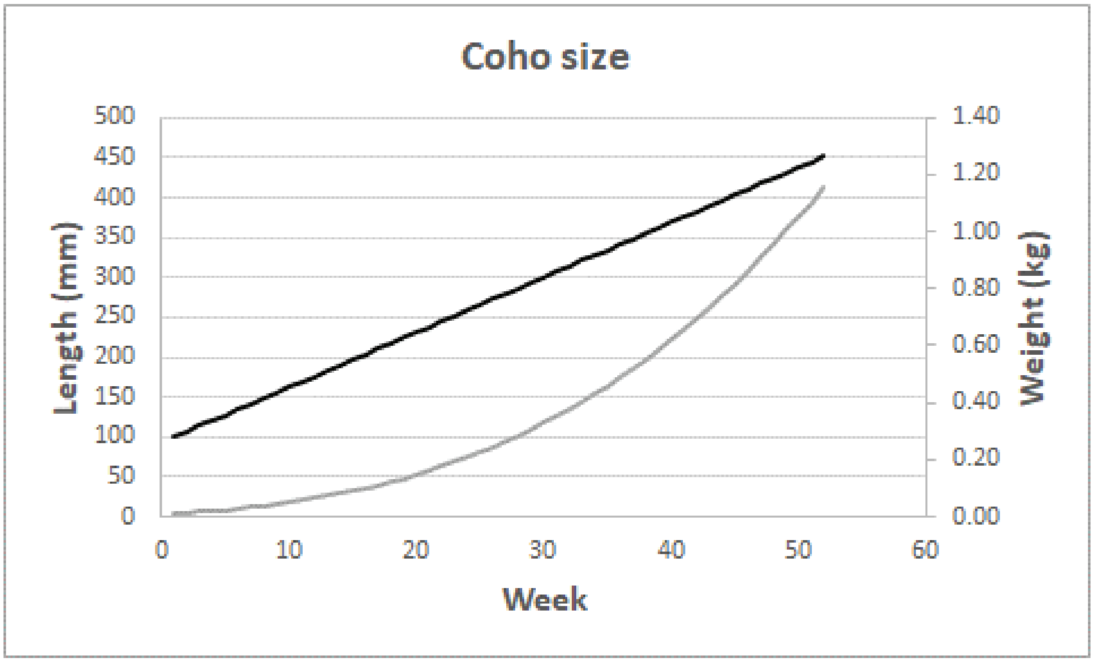


Figure B2: Coho salmon length (black) and weight (gray) over time for the harbour seal predation model.

Appendix C

C.1 Logistic growth model

C.1.1 Model structure and parameter estimation

In addition to the full age-structured model, historic abundance of harbour seals in British Columbia was assessed using a state-space version of the theta-logistic growth model (Pella and Tomlinson 1969, Jeffries et al. 2003):

$$N_{t+1} = \left[N_t + rN_t\left(1 - \left(\frac{N_t}{K}\right)^{\theta}\right) - C_t\right] exp(\varepsilon_t)\,, \qquad \text{(Eq. C1)}$$

where N_t is the population size in year t; r is the intrinsic population growth rate; K is the population carrying capacity; C_t is the number of animals harvested, and θ is the parameter that controls the maximum net productivity level of the population (Brown et al. 2005); when $\theta = 1.0$, Eq. C1 is the standard logistic growth model. ε_t are the annual process error deviations, which are assumed to be normally distributed, $\varepsilon_t \sim Normal(0, 0.05)$. Because the standard parameterization of the theta-logistic model often results in strong correlations between r and K during the parameter estimation process, we re-parameterized Eq. C1 according to Monnahan et al. (2014):

$$N_{t+1} = \left[N_t + rN_t\left(1 - \left(\frac{r\theta N_t}{MSY(\theta + 1)^{1/\theta+1}}\right)^{\theta}\right) - C_t\right] exp(\varepsilon_t), \qquad \text{(Eq. C2)}$$

which is possible because $MSY = rK\theta/(\theta + 1)^{1/\theta+1}$. We then set $K = MSY(\theta + 1)^{1/\theta+1}$. The model was initialized in 1939, at which time the abundance for this year was assumed to be unknown, so it was estimated it as a free parameter, N_{1939}. Finally, we assumed that the [observation] error associated with abundance estimates from aerial surveys were log-normally distributed, and formulated the following objective function for the fitting the model:

$$NLL = -nlog_e(\sigma_{Obs}) + c_3 \qquad \text{(Eq. C3)}$$

Where c_3 is a constant that can be ignored, n is the number of observations, and σ_{obs} is the observation error standard deviation:

$$\sigma_{Obs} = \sqrt{\frac{\sum_{i=1}^{n} log_e(x_i/q_{mle}/N_i)^2}{n}} \qquad \text{(Eq. C4)}$$

x_i is the observed total abundance, N_i is the predicted total abundance from the population model described above, and q is the "observability coefficient" for the total abundance of harbour seals:

$$q = exp\left[\frac{\sum_{i=1}^{n} log_e(x_i/N_i)}{n}\right] \qquad \text{(Eq. C5)}$$

A normal prior distribution with a mean of 1.0 and a C.V. of 0.15 was imposed on q.

AD Model Builder (ADMB) software (Fournier et al. 2012) was used to minimize the objective function (likelihood + priors). ADMB uses a quazi-Newton optimization algorithm to estimate model parameters, and calculates standard errors associated with those parameters using the Delta-method.

C.1.2 Model selection

We compared two versions of the theta-logistic model using Akaike Information Criteria (AIC) (Burnham and Anderson 2002). The simplest candidate model was Eq. C1 with θ fixed at 1.0; this is the standard logistic growth model (Jeffries et al. 2003). The second candidate model allowed θ to be estimated as a free parameter in the MLE procedure, in addition to r, K, and N_{1939}. The two models were compared using the following information criterion for small samples:

$$AICc_i = -2log(L_i) + 2m_i + \frac{2m_i(m_i + 1)}{(n - m_i - 1)} \qquad \text{(Eq. C6)}$$

where L_i is the likelihood of model *i, m* is the total number of estimated parameters, and *n* is the number of data points (aerial surveys) used in the MLE procedure. Finally, we selected the best model for our analysis by comparing the AIC weights of the two models:

$$\bar{w}_i = \frac{exp(-0.5\Delta_i)}{\sum_{i=1}^{M} exp(-0.5\Delta_i)} \qquad \text{(Eq. C7)}$$

where $\Delta_i = AICc_i - minAICc$, and *M* is the number of candidate models. Results of the model comparison are displayed in Table C4.

C.2 Growth rate as a function of animals sterilized

Projecting the response of the harbour seal population to lethal removals with the logistic growth model was relatively straightforward— we simply subtracted the annual number of animals killed directly from the current population size, assuming no implementation error. In contrast, using the logistic growth model to estimate the population response to contraception was more complicated without an explicit parameter and/or function for population fecundity. Thus, we modeled changes in fecundity from sterilization by formulating a relationship between the proportion of females sterilized and the intrinsic population growth rate (r) that was estimated from the surplus production model (Eqs. C1-C2). Using information from life tables for the harbour seal population that are available in previous studies (Olesiuk 1993; Tables C1-

C2), we used the following set of equations to calculate the reduction in population growth rate (r) as a function of increasing numbers of sterilized mature female seals.

First, we calculated the relative contribution to the reproductive capacity of the total population at each age, which is the product of female maturity-at-age (M_a), survivorship (l_a), and the size/mass (G_a). The total reproductive capacity of the population is the sum of all contributions, across ages:

$$\varphi = \sum_{i=0}^{A} M_a l_a G_a \tag{Eq. C8}$$

Following Dorn (2002), the maximum recruitment rate of the population (α), assuming a Beverton-Holt type relationship for recruitment, is:

$$\alpha = \varphi \frac{1-h}{4h} \tag{Eq. C9}$$

where h is the "steepness" parameter, which is the recruitment level when the population is at approximately 20% of its unexploited biomass. With α we can calculate the maximum recruitment per unit of female body mass (kg) for the population:

$$\frac{R}{F} = \frac{1}{\alpha} \tag{Eq. C10}$$

The relative contribution to recruitment, by age, can be calculated by multiplying the per unit recruitment potential by the mass-at-age:

$$\frac{R}{F_a} = G_a\left(\frac{R}{F}\right) \tag{Eq. C11}$$

To estimate the population growth rate at different proportions of the female population sterilized, we used the following equation, which calculates the recruitment potential for the population, given the proportion of sterile females (p):

$$Prod = \sum_{a=0}^{A} \left[l_a \left(\frac{R}{F_a} \right) M_a (1 - p) \right] exp^{(-ar)} \tag{Eq. C12}$$

By minimizing the penalty function $(1 - Prod)^2$ over different levels of sterilization in the population, we were able to estimate the adjusted population growth rate (r^*) that would mimic the loss in fecundity associated with the particular management alternative (Fig. C4). Thus, if a non-lethal management alternative was implemented in year t that corresponded with p_t of the total non-pup females being sterilized, r^* would be substituted for r in Eq. C2 in the next year$(t + 1)$.

Table C1: Life tables for the British Columbia harbour seal population, modified from Olesiuk (1993). Shown, by age, is fecundity, age-at-maturity, annual survival rate, and annual instantaneous mortality rate.

Age	Fecundity	Female maturity	Male maturity	Female survival	Male survival	Female M	Male M
0	0.00	0.00	0.00	0.73	0.73	0.31	0.31
1	0.00	0.00	0.00	0.90	0.85	0.11	0.16
2	0.00	0.00	0.00	0.90	0.85	0.11	0.16
3	0.29	0.36	0.06	0.90	0.85	0.11	0.16
4	0.66	0.83	0.29	0.90	0.85	0.11	0.16
5	0.79	1.00	0.53	0.90	0.85	0.11	0.16
6	0.91	1.00	1.00	0.90	0.85	0.11	0.16
7	0.91	1.00	1.00	0.90	0.85	0.11	0.16
8	0.91	1.00	1.00	0.90	0.85	0.11	0.16
9	0.91	1.00	1.00	0.90	0.85	0.11	0.16
10	0.91	1.00	1.00	0.90	0.85	0.11	0.16
11	0.91	1.00	1.00	0.90	0.85	0.11	0.16
12	0.91	1.00	1.00	0.90	0.85	0.11	0.16
13	0.91	1.00	1.00	0.90	0.85	0.11	0.16
14	0.91	1.00	1.00	0.90	0.85	0.11	0.16
15	0.91	1.00	1.00	0.90	0.85	0.11	0.16
16	0.91	1.00	-	0.90	-	0.11	-
17	0.91	1.00	-	0.90	-	0.11	-
18	0.91	1.00	-	0.90	-	0.11	-
19	0.91	1.00	-	0.90	-	0.11	-
20	0.91	1.00	-	0.90	-	0.11	-
21	0.91	1.00	-	0.90	-	0.11	-
22	0.91	1.00	-	0.90	-	0.11	-
23	0.91	1.00	-	0.90	-	0.11	-
24	0.91	1.00	-	0.90	-	0.11	-
25	0.91	1.00	-	0.90	-	0.11	-

Table C2: Extended life-history information for the British Columbia harbour seal population, which includes modified information from Olesiuk (1993). Shown, by age, size (mass), survivorship, and several quantities related to reproduction/recruitment that were used to calculate growth rates for the population.

Age	Female mass (kg)	Male mass (kg)	Female s'ship	Male s'ship	Relative size	Recruits per female	Prod.
0	24.00	24.00	1.00	1.00	0.00	0.19	0.00
1	29.30	29.30	0.73	0.73	0.00	0.23	0.00
2	36.00	38.90	0.66	0.62	0.00	0.28	0.00
3	43.90	48.90	0.59	0.53	9.34	0.34	0.06
4	50.00	57.50	0.53	0.45	22.09	0.39	0.12
5	54.50	64.50	0.48	0.38	26.10	0.42	0.13
6	57.90	70.20	0.43	0.32	24.96	0.45	0.11
7	60.20	74.60	0.39	0.28	23.35	0.47	0.10
8	62.00	78.10	0.35	0.23	21.65	0.48	0.08
9	63.20	80.80	0.31	0.20	19.86	0.49	0.07
10	64.00	82.80	0.28	0.17	18.10	0.50	0.06
11	64.60	84.40	0.25	0.14	16.44	0.50	0.05
12	65.00	85.50	0.23	0.12	14.89	0.50	0.04
13	65.30	86.40	0.21	0.10	13.46	0.51	0.03
14	65.50	87.10	0.19	0.09	12.15	0.51	0.03
15	65.60	88.00	0.17	0.08	10.96	0.51	0.02
16	65.70	-	0.15	-	9.87	0.51	0.02
17	65.80	-	0.14	-	8.90	0.51	0.02
18	65.90	-	0.12	-	8.02	0.51	0.01
19	65.90	-	0.11	-	7.22	0.51	0.01
20	65.90	-	0.10	-	6.50	0.51	0.01
21	65.90	-	0.09	-	5.85	0.51	0.01
22	65.70	-	0.08	-	5.25	0.51	0.01
23	66.00	-	0.07	-	4.74	0.51	0.00
24	66.00	-	0.06	-	4.27	0.51	0.00
25	66.00	-	0.06	-	3.84	0.51	0.00

Table C3: Model comparison of candidate age-structured models with different values of non-pup vulnerability (Vul.) for before and after 1915. Shown are the negative log likelihoods, and small-sample AIC (AICc), and the AIC weights ($\bar{w}$) for each candidate model in parentheses. The best-performing model (highest $\bar{w}$) is highlighted in bold.

	Pre-1915 vul.		
Post-1915 vul.	**0.40**	**0.50**	**0.60**
0.80	53.5 (115; 0.00)	54.9 (117; 0.00)	52.8 (113; 0.00)
0.90	53.0 (114; 0.00)	53.1 (114; 0.00)	50.9 (109; 0.04)
1.00	61.3 (130; 0.00)	**47.5 (103; 0.93)**	51.0 (110; 0.03)

Table C4: Summary of model selection criteria for the two theta-logistic models considered in this analysis. Shown are the number of estimated parameters, the negative log likelihood (NLL), small-sample AIC (AICc), and the AIC weights ($\bar{w}$) for each candidate model. The $\bar{w}$ of the best-performing model is shown in bold.

Model	**Parameters**	**NLL**	**AICc**	$\bar{w}$
Fixed θ	3	219	446	0.00
Free θ	4	164	338	**1.00**

Table C5: Posterior estimates of parameters for the best-performing logistic-growth model for British Columbia harbour seals. Also shown are the standard deviations (SD) for each parameter estimate and the 95% probability intervals.

Parameter	**Posterior mode**	**SD**	**95% PI**
K	99,882	9,550	81,164-118,600
r	0.087	0.011	0.065-0.109
θ	2.79	0.27	2.26-3.32
N_{1939}	50,274	3,520	43,375-57,173
q	1.10	-	-

Table C6: Median number of years to achieve target abundance (50,000) under each management scenario, for each model. Annual numbers of sterilized adult females are columns and annual lethal removals (kills) are in table rows. Each estimate is based on 1,000 simulations. Scenarios where the target abundance was not achieved was left blank.

	Sterilizations				
Kills	0	2500	5000	7500	10000
	Base age-structured model				
0	-	-	23	16	15
5000	-	15	11	9	8
10000	9	7	7	6	6
15000	5	5	5	5	5
20000	4	4	4	4	4
	Alternative age-structured model				
0	-	-	20	16	15
5000	-	11	9	8	7
10000	6	6	5	5	5
15000	4	4	4	4	4
20000	3	3	3	3	3
	Logistic model				
0	-	-	-	-	-
5000	-	-	-	-	20
10000	8	8	7	7	7
15000	5	5	5	5	5
20000	4	4	4	4	4

Table C7: Median minimum and maximum percent deviations from target abundance (50,000) under each management scenario, for each model. Deviations are calculated for years after the target abundance is achieved. Annual numbers of sterilizations of adult females are columns and annual lethal removals (kills) are in table rows. Each estimate is based on 1,000 simulations. Scenarios where the target abundance was not achieved was left blank. Scenarios where the maximum negative deviation from the target abundance is less than or equal to minus five percent are shown in bold text.

	Sterilizations				
Kills	0	2500	5000	7500	10000
	Base age-structured model				
0	-	-	-10/-2	-12/0	-12/2
5000	-	**-4/0**	-20/0	-20/-2	-18/-2
10000	**0/4**	-6/2	-18/0	-24/0	-24/-2
15000	-8/4	-10/2	-12/0	-28/0	-26/-2
20000	-14/4	-12/2	-14/0	-30/-2	-30/0
	Alternative age-structured model				
0	-	-	-8/-2	-8/2	-8/4
5000	-	**-2/2**	-16/0	-12/0	-16/0
10000	**-4/6**	**-2/2**	-16/0	-22/2	-20/0
15000	-12/10	-12/6	-12/2	-22/2	-22/0
20000	**0/8**	**0/4**	-34/4	-40/2	-40/2
	Logistic model				
0	-	-	-	-	-
5000	-	-	-	-	0/2
10000	**0/4**	**-2/4**	**-2/2**	**-4/2**	**-6/2**
15000	-10/4	-10/4	-12/4	-12/2	-10/2
20000	-14/4	-14/4	-16/4	-14/2	-16/2

Table C8: Coefficient of variation (CV) of seal abundances over the 25-year period once the target abundance (50,000) has been reached under each management scenario, for each model. Annual numbers of sterilized adult females are columns and annual lethal removals (kills) are in table rows. Each estimate is based on 1,000 simulations. Scenarios where the target abundance was not achieved was left blank. Scenarios where the CV of abundance is less than or equal to 0.05 are shown in bold.

	Sterilizations				
Kills	0	2500	5000	7500	10000
	Base age-structured model				
0	-	-	**0.04**	**0.05**	**0.05**
5000	-	**0.01**	0.09	0.08	0.06
10000	**0.01**	**0.02**	0.08	0.11	0.09
15000	**0.03**	**0.03**	**0.04**	0.12	0.09
20000	**0.04**	**0.03**	**0.05**	0.13	0.12
	Alternative age-structured model				
0	-	-	**0.03**	**0.04**	**0.05**
5000	-	**0.01**	0.07	**0.04**	0.06
10000	**0.02**	**0.01**	0.06	0.09	0.07
15000	**0.04**	**0.04**	**0.04**	0.09	0.08
20000	**0.01**	**0.01**	0.14	0.20	0.19
	Logistic model				
0	-	-	-	-	-
5000	-	-	-	-	**0.01**
10000	**0.01**	**0.02**	**0.01**	**0.02**	**0.02**
15000	**0.03**	**0.03**	**0.04**	**0.04**	**0.03**
20000	**0.04**	**0.04**	**0.05**	**0.05**	0.06

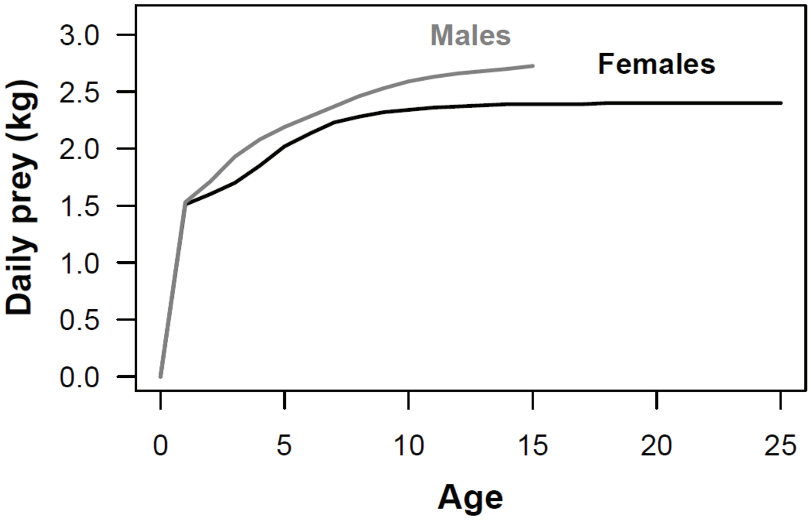


Figure C1: Daily prey requirements of harbour seals in the Strait of Georgia, by age (modified from Olesiuk 1993). The gray series shows the relationship for male seals (ages 0-15), while the black series shows the relationship for female seals (ages 0-25).

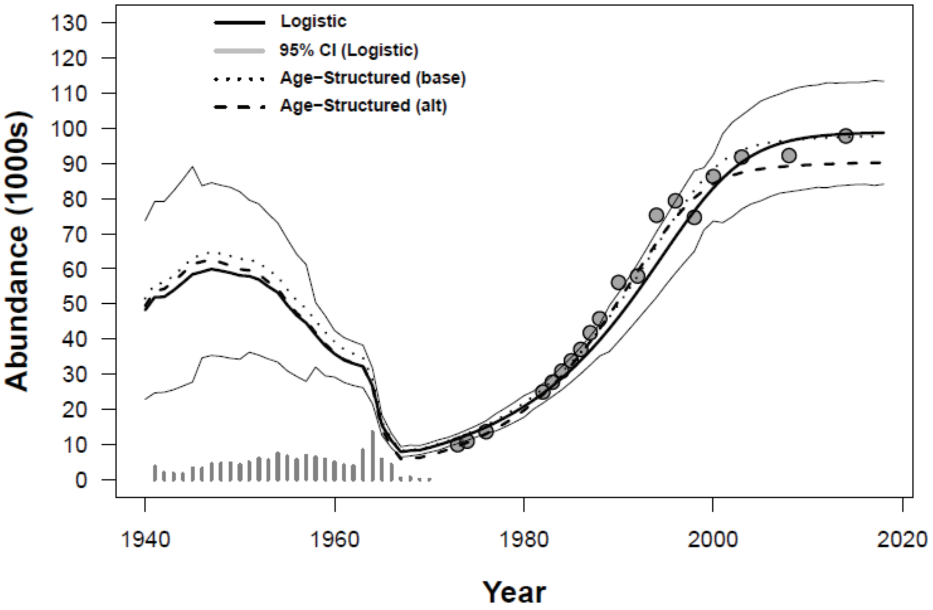


Figure C2: Model-predicted harbour seal abundance in British Columbia from 1940-2018. The solid lines depict the estimated abundance using the theta-logistic model, while the dotted and dashed lines show the mean predicted abundance from the base case and alternative full sex- and age-structured models. Observed abundances are shown with solid circles, and the annual number of animals killed are shown by gray bars.

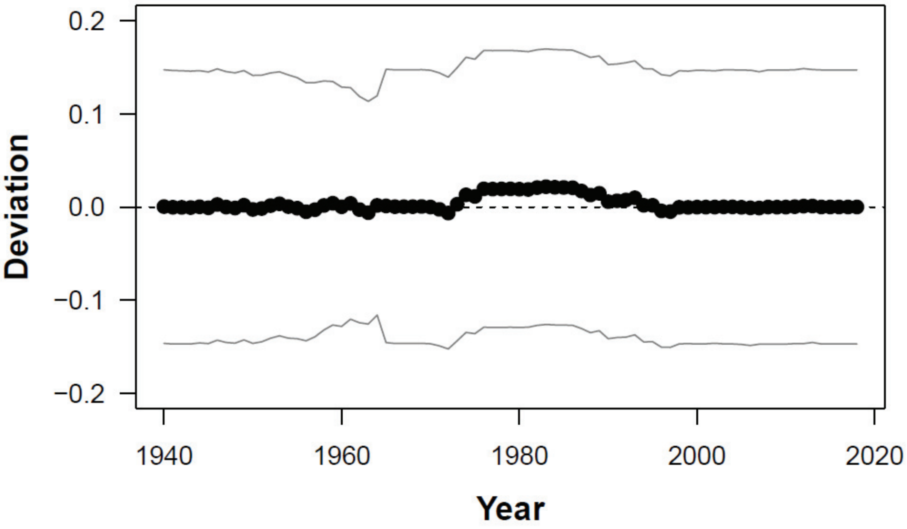


Figure C3: Estimated annual recruitment deviations between 1940 and 2018 for the age-structured harbour seal population model. The 95% probability intervals are depicted by the thin gray lines.

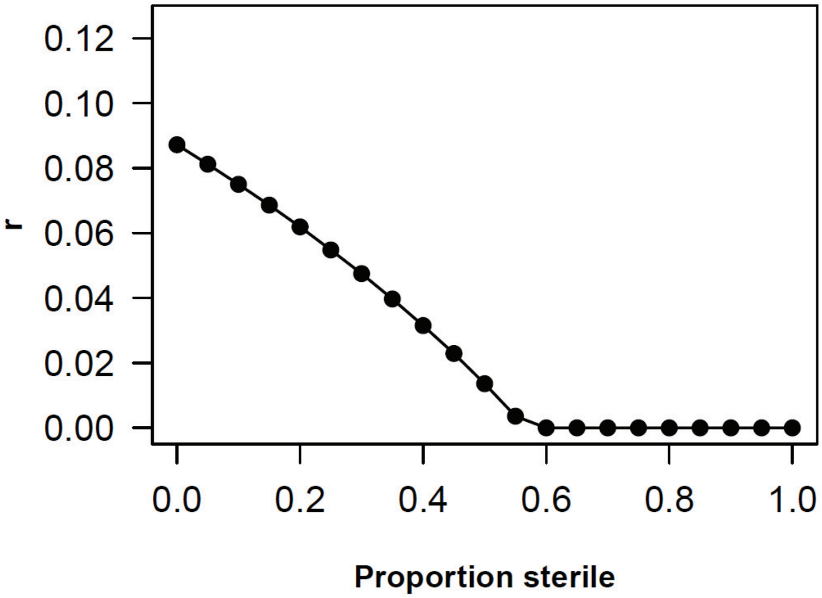


Figure C4: Population growth rate (y-axis) of the British Columbia harbour seal population as a function of the proportion of sterilized non-pup females (x-axis).