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Comparing lethal and non-lethal methods of active population control for harbor seals in British Columbia

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Abstract

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 controlling pinniped population abundance using lethal measures such as harvesting or by non-lethal means like contraception could recover fish populations. It is unclear, however, 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 how quickly harbor seal (*Phoca vitulina*) abundance in British Columbia, Canada, could be reduced by 50%, through combinations of lethal removals and sterilization of adult females. Models were fit to seal abundance, demographic, and harvest data collected between 1879 and 2014. Simulation modeling suggests reliance on contraception exclusively is unlikely to reduce the current harbor seal population (numbering ~100,000) by 50% within 25 years, and would result in more variable outcomes, compared to lethal removals. Contraception could be combined with harvesting to maintain a target abundance of harbor seals (although captive studies with harbor 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 harbor seal numbers.

KEYWORDS

British Columbia, harbor seal, integrated population model, population control, sterilization

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, Reidy 2019), or compete with other species of high conservation concern (Williams et al. 2011, Chasco et al. 2017).

Harbor 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 (Stanley et al. 1996). On the west coast of North America, harbor seal populations increased exponentially following protection from (bounty) hunting and government-led culling programs in the early-1970s, then leveled off in the 1990s (Jeffries et al. 2003, Brown et al. 2005, Olesiuk 2010). In British Columbia, Canada, prolonged hunting and culling efforts in the nineteenth and twentieth centuries were not controlled by any specific management policy, and have been preceded by some ambient level of hunting by First Nations groups (McKechnie 2013).

Coincident with the recovery of harbor 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. 2019, Sobocinski et al. 2020). Chinook and coho salmon, and steelhead are valuable components of fisheries (commercial, recreational, and Indigenous), and are of high cultural significance to Indigenous North Americans. An important role Chinook salmon serve in the contemporary ecosystem is as 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 of high importance to reducing risk of extinction of this population of killer whales (Lacy et al. 2017, Wasser et al. 2017). In response to the perceived effect of predation on Chinook salmon populations, and the potential competition with southern resident killer whales, some stakeholders have advocated reducing the abundance of harbor seals in British Columbia and Washington, USA, through permitted culling, sustainable harvest (Southern Resident Orca Task Force 2018, Pacific Balance Pinnipeds Society [PBPS] 2019), or both.

The large numbers of harbor 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 harbor 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 complementary management strategy to hunting and culling, and is viewed by some as a humane means of controlling wildlife populations (Kirkpatrick et al. 1996, 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 (Palmer et al. 2018, Yang et al. 2023), with one of the most common applications in mammal species being immuno-contraception intended to sterilize females. Such methods have been applied to many species and include rabbits, opossums, badgers, foxes, cats, dogs, pigs, white-tailed deer (*Odocoileus virginianus*), elk (*Cervus canadensis*), bison (*Bison bison*), and horses (*Equus caballus*). Successful applications to wild and feral populations of these species have been achieved in Asia, North America, and Australia (Messai and Cowan 2014).

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 (Messai and Cowan 2014). Large field applications have also yielded mixed results, ranging from completely unsuccessful (Twigg et al. 2000) to marked reductions in abundance and population growth rate (Kirkpatrick and Turner 2008, Rutberg and Naugle 2008).

Among pinnipeds, 2 primary forms of contraception have been 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, Canada), 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 vaccines have not yet been administered to harbor seals in an experimental setting, but is expected to result in similar outcomes to those seen in grey seals (M. A. Fraker, SpayVac®, personal communication).

Before allocating resources to test the efficacy of zona pellucida immuno-contraception vaccines on harbor 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., culling and hunting). One way of doing so is by combining 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 harbor seal population in British Columbia, we compared expected outcomes of lethal 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 (i.e., no targeted demographic) harvesting that has been proposed (PBPS 2019). 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.

STUDY AREA

This study pertains to the harbor seal population in the Canadian province of British Columbia (944,735 km^2). Major marine geographic regions of the eastern Pacific Ocean relevant here include the mainland coast of British Columbia, Haida Gwaii (formally the Queen Charlotte Islands), the Strait of Georgia, and the Strait of Juan de Fuca.

Coastal geology is composed primarily of rocky shorelines and mountainous fjords on both the outer and inner coasts, in addition to numerous shallow, muddy bays and estuaries within the Salish Sea region (Strait of Georgia and Strait of Juan de Fuca). Climate along coastal British Columbia is generally mild and rainy because of the influence of the North Pacific Current.

Land use in British Columbia varies considerably, from dense urban and residential areas near the major population centers of Vancouver and Victoria, to remote rainforests and mountainous terrain along the central coast, Vancouver Island, and interior. These remote areas are home to a wide variety of fauna. Terrestrial mammals include bears (*Ursus* spp.), deer (*Odocoileus* spp.), elk, moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), wolves (*Canis lupus*), cougars (*Puma concolor*), and others. Marine mammal species include numerous healthy populations of harbor seals, sea lions, otters, whales, dolphins, and porpoises. The time period of our modeling study extends from around 1879 to 2014, which is when several data sets were collected.

METHODS

Harbor seal data

We used estimates of seal abundance, historical kill records, and estimates of age composition to develop an age- and sex-structured population dynamics model of the harbor seal population in British Columbia. There were 19 abundance estimates available from aerial surveys of harbor seal haul-outs in British Columbia, which were performed periodically between 1973 and 2014 (Olesiuk 2010, Majewski and Ellis 2022; Table 1). Kill records from hunting and culling programs in the late-nineteenth and twentieth centuries were summarized by Olesiuk (2010). Because the number of recorded pelts and bounties likely underestimated the number of animals actually killed because of unrecoverable carcasses, Olesiuk (2010) assumed 62% of animals killed were accounted for. Additionally, because 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 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). We used these 3 data sets, along with prior distributions on several parameters, to fit the population model using a Bayesian approach.

Population dynamics models

The primary population dynamics model developed for this study is a state-space age- and sex-structured model that estimates the abundance of each age-sex group on an annual time step between 1879 and 2018. The state-space framework 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 deviates from recruitment. In addition to the sex- and age-structured model, we developed a simpler logistic growth model for the harbor seal population, which we fit to the same abundance data. We developed a simpler model 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 (see Supporting Information).

In the age- and sex-structured model, the maximum age for each sex (A^s) modeled was 25 for females and 15 for males; we assumed the small numbers of older animals fell into these maximum age groups (Table 2).

TABLE 1 Estimated and observed annual abundances of harbor seals in British Columbia, Canada, 1973–2014. We calculated observed abundances from aerial survey data in Olesiuk (2010) and adjusted them by the observability coefficient (q), whereas we obtained estimated abundances from the best-performing age-structured population model.

Year	Abundance	
	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

We assumed the harvested population in 1879 was at a stable age distribution and initialized the population model with the following equations:

$$N_{1,a}^{s} = \gamma^{s} N_{1879} s_{a}^{s(a-1)} \left(1 - s_{a}^{s}\right)(1 - v_{a} U_{t}) \quad 1 \leq a < A^{s} \tag{1}$$

$$N_{1,a}^{s} = \gamma^{s} N_{1879} s_{a}^{s(A-1)} (1 - v_{a} U_{t}) \quad a = A^{s} \tag{2}$$

Where N is the harvested population, v_a and U_t are the vulnerability at age a and harvest rate in year t, and 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:

$$l_{a}^{s} = \begin{cases} 1 & a = 0 \\ l_{a}^{s} = l_{a-1}^{s} s_{a-1}^{s} & 0 < a < A^{s} \\ l_{a}^{s} = l_{a-1}^{s} s_{a-1}^{s} & a = A^{s} \end{cases} \tag{3}$$

TABLE 2 Summary of parameters used in the sex- and age-structured population model for harbor seals in the Strait of Georgia, British Columbia, Canada.

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	autoregressive term for recruitment deviates	Øigård and Skaug (2015)
Subscripts	t	1879:2018	Year	
	s	Female, male	Sex	
	a	1: A^s	Age	

We assumed that annual survival rates for pups (s_0 = 73%), females (s^{Female} = 90%), and males (s^{Male} = 85%) were 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 rate can be non-stationary over time, we also evaluated 2 alternative models: a version with female nd male survival rates 25% greater than the nominal rates and a version with rates 25% less than the nominal survival rates.

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

$$N_{t+1,a+1}^s = \begin{cases} N_{t,a}^s s_a^s (1 - v_a U_t) & 1 \le a < A^s \\ \left(N_{t,a}^s + N_{t,a-1}^s\right) s_a^s (1 - v_a U_t) & a = A^s \end{cases} \tag{4}$$

We calculated the annual harvest rate using the equation:

$$U_t = \frac{C_t}{N_t}, \tag{5}$$

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 set at 0.90.

We assumed annual pup production was the density-dependent process limiting population growth, and we described this process by a theta-logistic or Pella-Tomlinson relationship (Pella and Tomlinson 1969), where the number of pups that enter the population annually is a function of abundance relative to population carrying capacity. We believe this is a reasonable assumption, as population growth is likely limited by suitable habitat, prey availability, or both (Brown et al. 2005), and because pup production and survival in pinniped populations is often inversely related to animal density at haul-outs and pupping areas (Coulson and Hickling 1964, Bigg 1966, Breed et al. 2013). We assumed a 1:1 sex-ratio for pup production in each year (Bigg 1969):

$$N_{t,0}^{s} = 0.5\left(F_t \sum_{a=1}^{A^{Female}} f_a N_{t,a}^{Female}\right), \tag{6}$$

where f_a is the fecundity at age a (Table 2), and F_t is the time-varying birth rate:

$$F_t = \left[\left(1 - \frac{N_{t-1}}{K}\right)^{\theta}\right] exp(\varepsilon_t). \tag{7}$$

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: $\varepsilon_t \sim \text{Normal}(0, \sigma_{Rec})$. We estimated recruitment deviations only for pup production between 1940 and 2018, as the first year of observed data (age composition) was not 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 Equation 7, we also evaluated an alternate pupping function:

$$F_t = \left[1 - (1 - F)\left(\frac{N_{t-1}}{K}\right)^{\theta}\right] exp(\varepsilon_t), \tag{8}$$

where F is the pupping rate at carrying capacity (K; Skaug et al. 2007). Versions of the age-structured model that used Equation 8 were 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 Equation 7 as a pupping function.

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 2 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:

$$L_1 = -n\log_e(\sigma_{Obs}) + c_1, \tag{9}$$

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:

$$\sigma_{Obs} = \sqrt{\frac{\sum_{i=1}^{n} log_e(x_i/q/N_i)^2}{n}} \tag{10}$$

where x_i is the observed total abundance, N_i is the predicted 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 harbor seals:

$$q = \exp\left[\frac{\sum_{i=1}^{n} log_e(x_i/N_i)}{n}\right] \tag{11}$$

The normal prior distribution for q assumed a mean of 1.0 and a standard deviation of 0.15. We incorporated age-composition data from lethal sampling efforts in the 1960s (Bigg 1966, 1969) 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:

$$L_2 = -\sum_{s} \frac{25}{x_{1965}^{s}} \sum_{a=1}^{A^s} x_{1965,a}^{s} log\left[N_{t,a}^{s}\left(\sum_{a=1}^{A^s} N_{1965,a}^{s}\right)^{-1}\right] + c_2 \tag{12}$$

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. These samples were likely not random (e.g., bias in behavior of captured animals); therefore, 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. We minimized the objective function using the mle function (BFGS algorithm) in the stats4 package in the R Programming Environment (R Core Team 2017).

Comparison of lethal versus non-lethal population control

We used the posterior parameter estimates from the age-structured population model to simulate future harbor seal population dynamics over a range of population control scenarios. We tested 2 general population control methods: indiscriminate lethal harvest of pups and adults and contraceptive measures through vaccination of adult females. Indiscriminate harvest refers to removing animals without a specific bias towards sex or age. 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 $\rho = 0.70$ (Øigård and Skaug 2015). We performed 1,000 simulations for each scenario.

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

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, we 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 Equation 7:

$$N_{t,0}^{s} = 0.5 \quad \left[\left(F_t \sum_{a=1}^{A^{Female}} f_a N_{t,a}^{Female}(1 - p_t)\right) + \left(F_t \sum_{a=1}^{A^{Female}} f_a^{*} N_{t,a}^{Female} p_t\right)\right] \tag{13}$$

where p_t is the proportion of treated 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

$$N_t^{Sterile} = \begin{cases} V_t s^{Female}, & t = 2019 \\ \left(N_{t-1}^{Sterile} + V_t\right) s^{Female}, & t > 2019 \end{cases} \tag{14}$$

$V_{t,a}$ 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.

Under both lethal and non-lethal management options, we simulated the population dynamics of the harbor 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 (Figure 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. We evaluated scenarios where exclusively lethal or exclusively non-lethal methods were used and 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 harbor seal population, which we set at 50,000

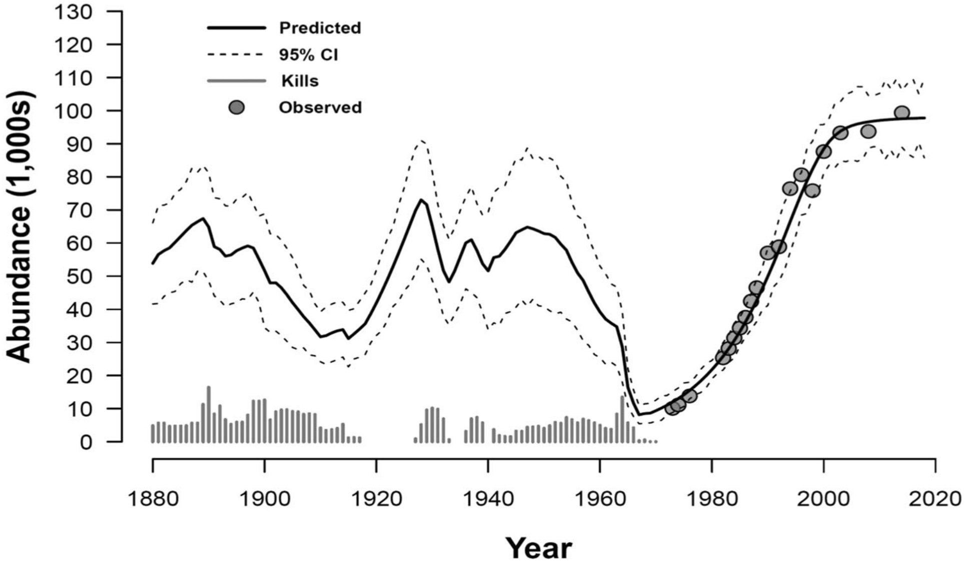

FIGURE 1 Predicted (solid line) and observed (circles) abundance of harbor seals in British Columbia, Canada, 1880–2018. The 95% probability intervals for estimated abundance are depicted by the dashed lines. The number of annual kills (bars) from records of hunting and culling (Olesiuk 2010) are shown along the x-axis.

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 was used, we evaluated 2 different implementations: a combination of lethal and non-lethal efforts occur simultaneously from the start of the management period and 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. We added the second approach to the analysis after preliminary simulation results suggested depletion of the seal population using contraception exclusively would require a large number of vaccines, which could be cost-prohibitive. Previous research on terrestrial species reported more realistic management scenarios may involve using contraception to suppress or maintain a population previously depleted through culling (Raiho et al. 2015).

RESULTS

Seal population dynamics

The best age-structured model used a value of 0.50 for the vulnerability of non-pups (before 1915; i.e., base case age-structured; Figure 1; Table 2). We evaluated 9 different models, with different assumptions regarding harvest vulnerability before and after 1915 (Table S3, available in Supporting Information). 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 (1879) of the time series through the mid-1990s, at which point the abundance began to approach an asymptote (Table 3; Figure S1, available in Supporting Information). The 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 (Figure 1; Figure S1). 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 (Figure S1). The model that considered 25% more natural mortality did not produce a stable solution.

When fit to the same abundance data as the base case age-structured model, the best-performing theta-logistic model showed the same general population dynamics from 1939–2018 (Figure S1). A theta-logistic model with θ as an estimated free parameter (corrected Akaike's Information Criterion [AIC_c] = 338) out-performed the basic logistic growth model where θ = 1 (AIC_c = 446). Uncertainty around annual population size in the decades before and up

TABLE 3 Parameter estimates for 2 sex- and age-structured models of the harbor seal population in British Columbia, Canada. Models were fit to several data sources collected between 1879 and 2014. 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	Definition	Base case	SD (Base case)	−25% M	SD (−25% M)
K	Carrying capacity	117,673	10,570	109,190	9,997
N_{1879}	Total abundance in 1879	49,825	3,745	44,832	3,018
θ	Pella-Tomlinson shape parameter	2.97	0.27	1.87	0.32
q_{mle}	Observability coefficient	1.08	-	1.15	-

until the mid-1960s was 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 similar for both model structures, the age-structured model estimated a higher carrying capacity (median = 117,673) relative to the theta-logistic model (median = 99,882; Table 3; Figure S2, available in Supporting Information).

Using the base case age-structured model, the estimated mean population size in 1879 was 49,825 seals (95% probability interval [PI]: 42,485–57,165; Figure 1). The seal population reached its minimum abundance in 1967 at 8,149 animals (95% PI = 5,391–10,906), a consequence of the high mortality rates that occurred throughout the decade (Figure 1). The current (2018) estimated abundance of harbor 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 (Figure S4, available in Supporting Information). The estimated observability coefficient (q_{mle}) for all 3 models was >1.00, which implies that either aerial surveys over-counted the actual numbers of adult harbor seals in the survey area or the factor applied by the Department of Fisheries and Oceans Canada to convert counts to the total population was positively biased. Previous research suggested that potential sources of observation error could be from immigration, emigration, or inclusion of pups in the adult counts (Olesiuk 2010).

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 (Figure S2). The estimated population proportions by age in 1965 showed a good fit to the observed data for females and males (Figure S3, available in Supporting Information). 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 (Figures 2–3). Specifically, the average age of adult females increased from 9.2 years to 11.5 years, while the mean age for males went from 6.1 years to 7.4 years (Figure 3). The maximum estimated kill rate for harbor seals in British Columbia

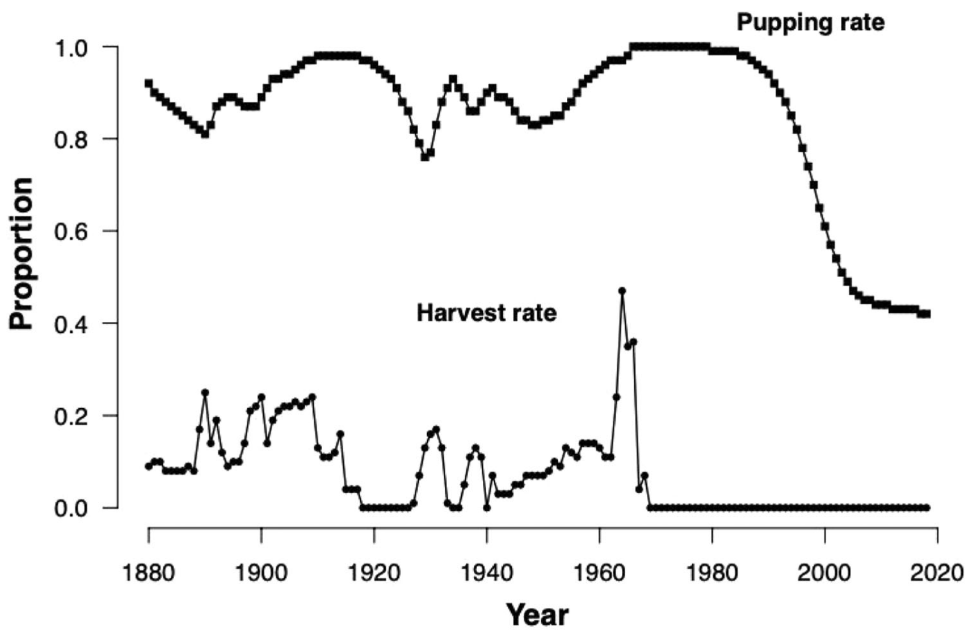

FIGURE 2 Estimated pupping rate (squares) in the population and harvest rates (circles) in the British Columbia, Canada, harbor seal population, 1880 and 2018.

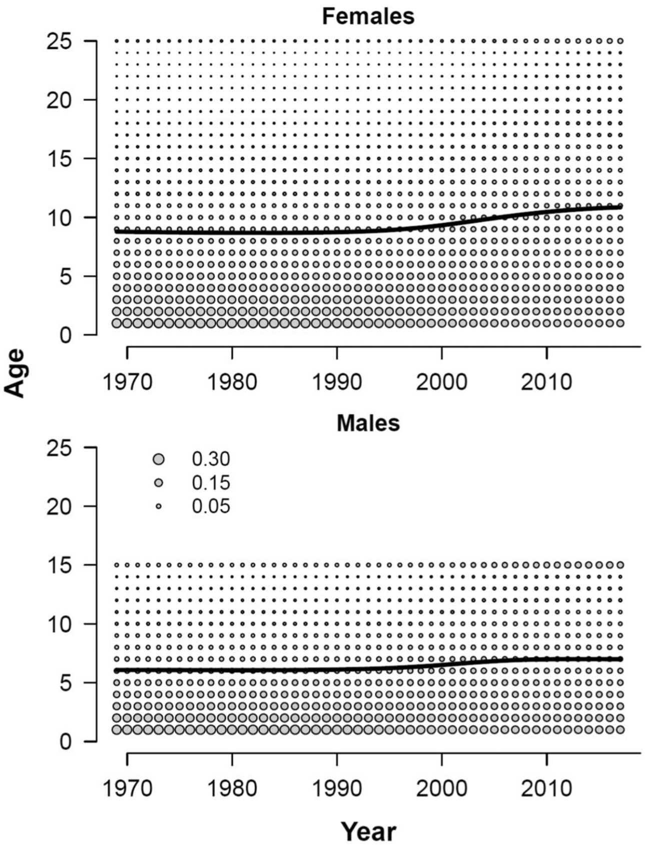

FIGURE 3 Bubble plots depicting proportions at age of British Columbia, Canada, harbor seals, 1970–2018. Separate plots for females (top) and males (bottom) are shown. The radius of circles are proportional to the fraction of the population at each age (*y*-axis). The solid black line shows the mean age of the population in each year.

occurred in 1964 at 47.2% (Figure 2). It is estimated that birth rates were highest during periods of intense harvest but declined steadily once the population was protected in the 1970s (Figure 2). Average age has been stable since the 2010s for males, while the average age of females appears to still be increasing (Figure 3).

Comparison of management alternatives

The future population dynamics of the harbor seal population were simulated under 9 different scenarios of active population control: 3 scenarios using varying levels of indiscriminate harvesting exclusively, 3 using fertility control exclusively, and 3 using a combination of lethal measures and fertility control from the first year of the management period (Figure 4). Simulations of these 9 scenarios suggest that adoption of lethal indiscriminate harvesting as a management alternative would require considerable effort to achieve the target depletion level (50,000 animals) within 10 years (Figure 4). For example, a simulated annual removal of 5,000 animals failed to achieve the target population level within 25 years (Figures 4–5; Figure S5, available in Supporting Information). 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 (Figures 4–5 and S5). Annual removals of 15,000 animals/year, which would be comparable to the annual largest efforts during the twentieth century, would reduce the population to the target abundance within

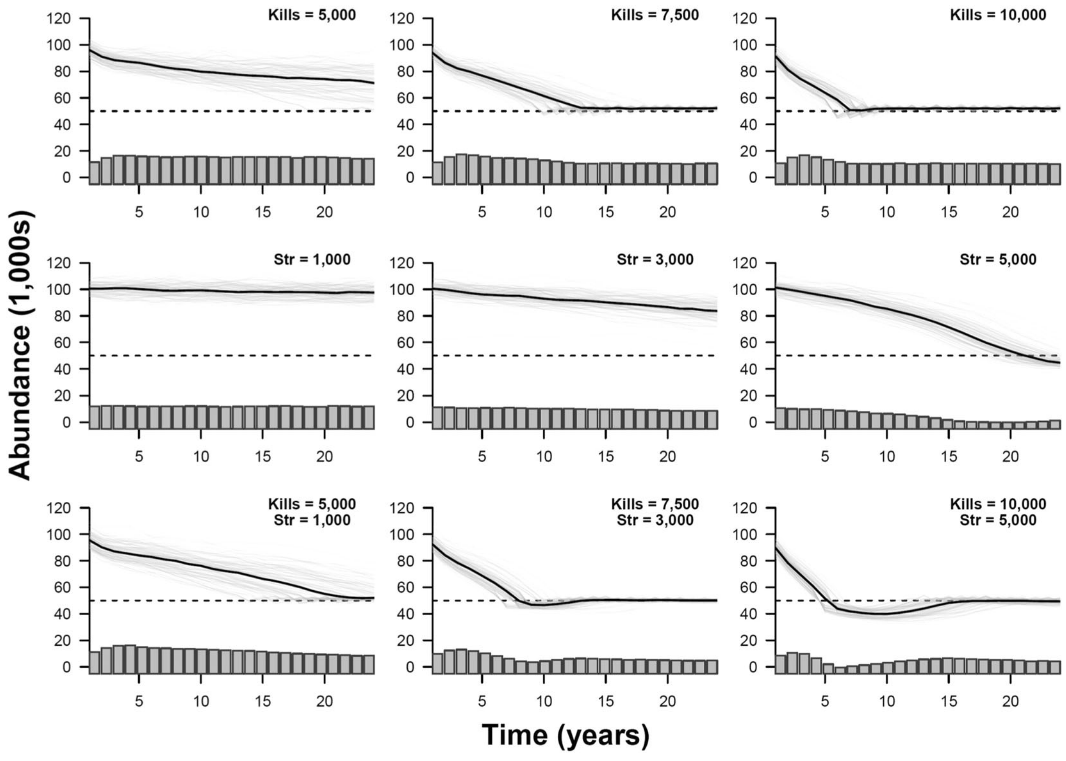

FIGURE 4 Projections of the British Columbia, Canada, harbor seal population under multiple population control scenarios using indiscriminate lethal removals (number removed each year [kills]) and fertility control measures (number of adult females sterilized each year [str]), and combinations of both. 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.

approximately 5 years, on average (Figure S5). Using non-lethal measures exclusively, between 4,000 and 5,000 females would need to be vaccinated annually to achieve the target abundance within 25 years (Figures S5 and 5). 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/year, there is a clear level of diminishing returns, with regard to decrease in population level per vaccination (Figure S5).

Management scenarios involving a simultaneous combination of harvesting and fertility control reduced the number of years necessary to achieve the target abundance, compared with those only using lethal methods. (Figures 4 and S5). 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 (Figure 4). Similarly, an annual combination of 5,000 culls and 5,000 vaccinated females would achieve target abundance within approximately 10 years of management (Figure 4 and S5). 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 (Figure S6, available in Supporting Information). 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 (Figure S6). It appears that annual efforts involving the vaccination of at

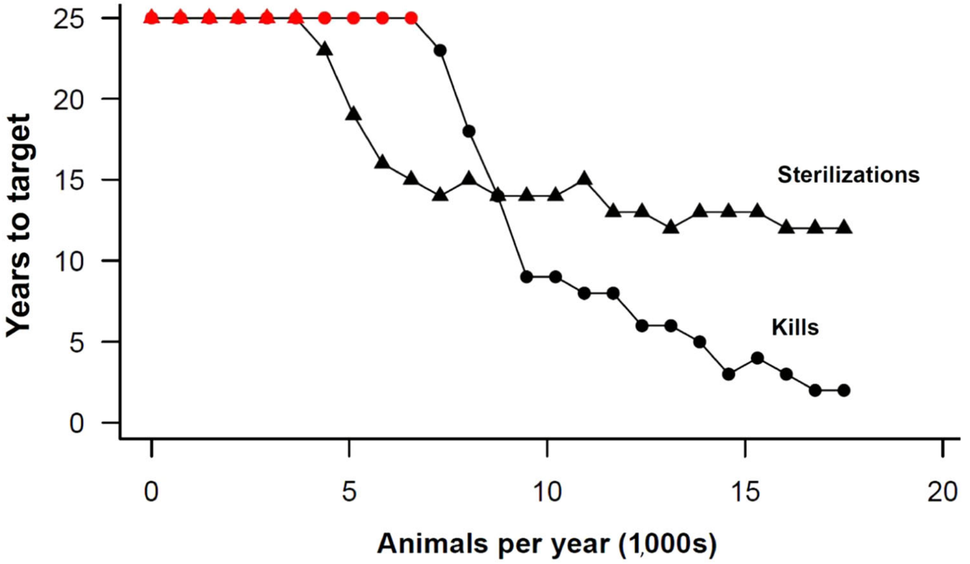

FIGURE 5 Median number of years to achieve the target abundance of 50,000 harbor seals in British Columbia, Canada, as a function of annual kills from indiscriminate lethal removals and annual sterilizations of adult females (triangles). Estimates of years to target abundance are based on 1,000 simulations 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 (2019–2044) are in red.

least 5,000 females would be required for scenarios where fertility control was implemented after target abundance was reached through harvesting.

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 (Figure S5; Table S7, available in Supporting Information). Use of contraception also resulted in higher variation around the target abundance than scenarios that only used lethal methods (Figure S5; Table S8, available in Supporting Information). 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/year) had higher variation around the target abundance, and much higher negative deviations from that level (Figure S5; Table S8).

Generally, the base case and alternate age-structured models produced similar population responses across the various management scenarios simulated in this analysis (Figures S5–S6). More specifically, for 13 of the 22 management scenarios (59%; Figure S5) where target abundance was achieved, the median difference between the 2 models in terms of number of years to target abundance was only 1 year (Table S6, available in Supporting Information). In all scenarios, the difference between the base and alternative age-structured models never exceeded 4 years. Because the base case version of the age-structured model estimated a higher current abundance of the harbor seal population, the time and effort needed to reach the target abundance was longer and higher compared to the alternate version (Figures S5–S6; Table S6). Compared with the age-structured models, the logistic model produced comparable outcomes in some scenarios but markedly different outcomes in others (Figures S5–S6; Table S6). Specifically, when management scenarios involved lethal methods exclusively, the logistic population model projected dynamics that were similar to the 2 age-structured models, particularly the base case (Figures S5–S6). 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 Figure S5). 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 (Figure S6).

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 be used to manage British Columbia's harbor seal population, which may be impeding the recovery of salmon species of high conservation concern (Chasco et al. 2017, Thomas et al. 2017).

Our simulation models suggest a considerable effort would be required to reduce the current harbor seal population to the 50% level proposed by some stakeholders, regardless of whether lethal or non-lethal measures are used. Using indiscriminate 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 >5,000 adult females annually. A combination of lethal and non-lethal methods could also be used effectively to deplete, then maintain the harbor 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, Croft et al. 2020). 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 higher magnitude than if lethal harvesting is undertaken.

Harbor seal population status in British Columbia

The base case age-structured population model we developed estimates the recent (2018) abundance of British Columbia harbor seals at 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 nineteenth and twentieth 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 abundance between 1930–1960 appear to be somewhat higher. Unlike previous work (Olesiuk 2010), 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 harbor seal prey. For example, the most recent bioenergetics models for harbor seals in the region (Howard et al. 2013) use 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 (Figure 3; Figure S4). Updating estimates of population demographics could reduce model uncertainty, and if lethal removals were to occur, a sampling program similar to the one that occurred in the 1960s could be implemented to achieve this (Reidy 2019).

Differences among population models

In addition to the base case formulation, we also fit an alternate version of the age-structured model and a logistic growth model to harbor 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, that 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 different results were produced in some management scenarios.

While all 3 of the models we developed suggest that the British Columbia harbor 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. Both variants of the age-structured model suggest carrying capacity probably lies between 110,000 and 120,000 animals. We expect recent (and future) aerial surveys of seal numbers by Department of Fisheries and Oceans Canada scientists will be important for reconciling the discrepancy between the estimates of the age-structured and logistic models.

The logistic model could not properly evaluate the potential biological consequences of non-lethal population control options, and the model 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 (Figures S5–S6; Table S6) because vaccination affected only the surplus production term, which was close to zero when abundance was close to carrying capacity (see Supporting Information). The logistic model also consistently underrepresented the population fluctuations that could be expected to occur after the target abundance was reached (Tables S7 and S8). If substantially overshooting the target abundance (e.g., deviations >−20% of the target) is unacceptable, the logistic model would fail to reveal the policy options where this could occur (Table S7).

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 ≥10,000; Table S6). The logistic model, however, 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 harbor 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 closed-loop or feedback control simulation evaluation (Punt et al. 2020).

Active population control of harbor seals

From the early-1970s, the British Columbia harbor 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) were removed in consecutive years (Figures 4–5 and S5). If indiscriminate harvesting were implemented at levels comparable to maximum efforts seen in the twentieth century, a reduction of 50% of the population could be achieved in <5 years (Figures 5 and S5).

We show that it may be possible to reduce the harbor seal population in British Columbia solely through fertility control; however, it would require a 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 ≥5,000 females to be vaccinated annually, for approximately 22–25 years. Vaccinating 10,000 females per year would achieve the same result in approximately 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 (Figure 5).

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 (Figure 4). Such a policy might be advantageous if managers aimed to use only non-lethal management options in areas close to human population centers, but reduced time-to-target prediction would hold only if animals mixed spatially.

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). An action involving lethal removals may also confer advantages in line with the goals of ecosystem-based fisheries management (Marshall et al. 2018).

Because the direct effects of lethal control occur immediately, it is far easier to track performance metrics (e.g., change in abundance or 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 (Figures 4 and S5–S6). Similarly, if there were undesirable, unintended ecosystem effects as a result of a reduction in the harbor seal population, a management action that uses lethal removals could be abandoned immediately, and recovery could commence beginning with the next cohort of pups (Figure S6, 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 because of the longevity of female harbor seals (20–25 years; Olesiuk 1993). Short of lethally removing infertile animals, managers would be left with few options to recover the population.

An example of an indirect ecosystem effect that has concerned some scientists is the potential effect a reduced harbor seal population would have on mammal-eating transient killer whales, which are thought to be thriving in British Columbia because of an abundance of prey (Ford et al. 2013, Shields et al. 2018, Trites and Rosen 2019, Trzcinski 2020). Harbor 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 harbor seal population. Previous researchers on killer whale foraging behavior suggest 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 effects on 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 (Figure 4).

In addition to effects on marine mammal-eating killer whales, unintended or indirect ecosystem effects should be expected in the wake of a 50% reduction of a large abundance predator (Lessard et al. 2005, Bowen and Lingard 2013). For example, resulting increases in abundances of seals' preferred prey could undermine effects to reduce natural mortality on juvenile salmon if said prey populations consume meaningful numbers of salmon themselves. Managers should also consider the potential change in behavior of harbor seals, which may impede accurate population monitoring efforts or increase the difficulty of harvesting or tagging efforts.

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 harbor 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.

The issue of legal constraints on seal harvesting in Canada has not been addressed in recent harvesting proposals (PBPS 2019), except that Steller sea lions (*Eumetopias jubatus*) are listed under the Canadian Species at Risk Act. First Nations peoples can now obtain permits to harvest seals, but only for food and ceremonial purposes, and may also be able to obtain permits to harvest sea lions because the Canadian Species at Risk Act listing does not prohibit all harvesting. As evidenced by commercial seal harvesting that has a long and continuing history in eastern Canada, there is no national legal policy like the United States Marine Mammal Protection Act, which prohibits harvesting (except under special circumstances). The Department of Fisheries and Oceans Canada has the ability to manage harvest of marine mammals, but revivals of such opportunities have been constrained (Reidy 2019, Ouchi et al. 2022). Existing proposals do not address transboundary movement of seals, which occurs (Peterson et al. 2012) but is unlikely to involve a high proportion of the Canadian population (Olesiuk 2010). At present, the legal implications of harvesting a protected transboundary stock of marine mammals are unclear.

MANAGEMENT IMPLICATIONS

Harbor seals in British Columbia could 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 the least expensive way to reduce the population within a reasonable time. If immuno-contraception with zona pellucida antigens is effective on harbor seals, this non-lethal method by itself could potentially within 2 decades, or in a decade in conjunction with lethal methods, effectively control the harbor seal population in British Columbia. A strictly non-lethal approach, however, if there is interest in considering it, would first require studies on captive populations to confirm the effectiveness of contraception on harbor seals.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

No issues related to the ethics of animal welfare were relevant to this study.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the main article and the supplementary material of this article.

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SUPPORTING INFORMATION

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