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ARTICLE

Evaluating management strategies for marine mammal populations: an example for multiple species and multiple fishing sectors in Iceland

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Abstract: A management strategy evaluation (MSE) is used to estimate success at achieving conservation goals for marine mammals while also aiming to minimize impacts on commercial fisheries. It is intended to improve understanding of US import rules that require countries exporting fish and fish products to the USA to adhere to marine mammal bycatch standards "comparable" to those used by the USA. The MSE framework is applied, for illustrative purposes, to export fisheries in Iceland that impact harbor porpoises (*Phocoena phocoena*), harbor seals (*Phoca vitulina*), and grey seals (*Halichoerus grypus*). Several management strategies are evaluated. The harbor porpoise population is estimated to be close to or above its maximum net productivity level (MNPL) and, according to the model, will continue to increase even if current levels of human-caused mortality are unchanged. In contrast, the grey seal and harbor seal populations are below MNPL, and bycatch mortality in the lumpfish (*Cyclopterus lumpus*) fishery will need to be reduced to allow them to recover to MNPL.

Résumé : Une évaluation des stratégies de gestion (ESG) est utilisée pour estimer le succès vers l'atteinte d'objectifs de conservation des mammifères marins visant aussi à minimiser les impacts sur les pêches commerciales. L'objectif est d'améliorer la compréhension des règles d'importation américaines qui exigent que les pays qui exportent des poissons et des produits du poisson vers les États-Unis respectent des normes concernant les prises accessoires de mammifères marins « comparables » aux normes utilisées par les États-Unis. Le cadre d'ESG est appliqué, à des fins d'illustration, aux pêches vouées à l'exportation en Islande qui ont des impacts sur les marsouins communs (*Phocoena phocoena)*, les phoques communs (*Phoca vitulina*) et les phoques gris (*Halichoerus grypus*). Plusieurs stratégies de gestion sont évaluées. Il est estimé que la population de marsouins communs se situe aux alentours ou au-dessus de son niveau de productivité nette maximum (NPNM) et, selon le modèle, qu'elle continuera d'augmenter même si les taux de mortalité causée par les humains demeurent inchangés. En revanche, les populations de phoques gris et de phoques communs sont sous leurs NPNM, et la mortalité associée aux prises accessoires dans la pêche à la grosse poule de mer devra diminuer pour permettre un retour au NPNM. [Traduit par la Rédaction]

Introduction

There is a long history of deliberate exploitation of marine mammals worldwide. Although commercial whaling and sealing have declined mainly due to a combination of regulation and resource depletion, many species of cetaceans, pinnipeds, and sirenians as well as sea otters (*Enhydra lutris*) and polar bears (*Ursus maritimus*) are still hunted for meat, skins, oil, bait, ivory, and predator control (Reeves 2018*a*). Moreover, there are substantial (and probably increasing) levels of incidental human-caused mortality (and (or) serious injury) of marine mammals. Most such mortality and serious injury results from entanglement, entrapment, or hooking in commercial fishing gear or entanglement in aquaculture nets and ropes (Kemper et al. 2003; Read 2005; Reeves et al. 2013). Read et al. (2006) estimated that at least several hundred thousand marine mammals die in this way each year, worldwide. Bycatch of marine mammals in fishing gear is the most certain and potent driver of human-caused population declines and the primary barrier to population recovery.

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Conservation concerns have led to calls for mitigating incidental impacts on marine mammals through the management and regulation of certain human activities at local, national, regional, and international levels (Reeves 2018*b*). Bycatch mortality (understood to encompass entanglement, entrapment, and hooking in or by gear) in commercial fisheries has been the subject of considerable research, development, and field testing of approaches to mitigation. A comprehensive global summary of this work was provided by Werner (2018) as part of an initiative of the Food and Agriculture Organization of the United Nations (FAO) Committee on Fisheries (FAO 2018). In the US, the Marine Mammal Protection Act of 1972 (MMPA) provides a legal and regulatory basis for assessing and mitigating the impacts of human activities, including commercial fishing, on marine mammals (Wade 1998; Roman et al. 2013).

Potential Biological Removal (PBR) and the Seafood Import Rule

The US National Oceanic and Atmospheric Administration (NOAA) evaluates the status of stocks (populations) and issues regulations for reducing incidental take (bycatch) of marine mammals in commercial fisheries. Within this regulatory framework, the PBR level is a reference point for managing bycatch (and other types of human-caused mortalities; Wade 1998). PBR is defined as the maximum number of marine mammals that humans can remove from a stock while allowing it to reach or maintain its optimum sustainable population (OSP) and is estimated based on monitoring data and assumptions about productivity. Even though PBR applies to all sources of human-caused removals, much of the focus of its application relates to the impact of commercial fisheries because US commercial fisheries are subject to specific requirements for monitoring and mitigating bycatch under the MMPA.

Just over 90% of the seafood consumed in the USA is imported (National Marine Fisheries Service 2018*a*). The Fish and Fish Product Import Provisions of the MMPA (50 CFR § 216.24; hereinafter referred to as the "Seafood Import Rule") require that imported fish and fish products be evaluated with respect to US standards, and the implementing regulations were issued in 2016. The regulations require countries that export fish and fish products to the US, and that are identified by NOAA as having fisheries that are documented or suspected to incidentally kill or seriously injure marine mammals (called "Export Fisheries"), to adhere to bycatch monitoring and mitigation standards "comparable" to those applied to US fisheries. A fishery can be categorized as an Export Fishery if NOAA has insufficient information on marine mammal bycatch rates or if the fishery's gear type is gillnet, trawl, longline, or purse seine, all of which are known to be commonly associated with marine mammal bycatch. Any country with one or more Export Fisheries is required to demonstrate that it has a regulatory program that addresses marine mammal bycatch in each such fishery. By 2021, the USA will make a comparability finding to determine whether that country's marine mammal bycatch program is comparable to that of the USA (Williams et al. 2016). If a foreign fishery fails the comparability finding, the fish or fish products from that fishery will be prohibited from entering the USA. Harvesting countries that fail to obtain approval by NOAA may refine their programs and receive a comparability finding.

Icelandic fisheries

Iceland is one of the largest fishing countries in the North Atlantic, with around 1.3 million tonnes (t) landed annually. In 2017, Iceland exported 22 590 t of fish to the USA (https://statice.is/; FAO 2018), which was landed by just over 1600 vessels, ranging from small inshore boats crewed by one to two persons up to large factory trawlers (MFRI 2018*a*).

The fisheries can be divided, in broad terms, into a groundfish fishery (roundfish and flatfish) using bottom trawls, longlines, jiggers, gillnets, and demersal seines and a pelagic fishery mainly using pelagic trawls and purse seines. The primary target of the groundfish fishery is Atlantic cod (*Gadus morhua*), and while bottom trawls are used to catch cod offshore, longlines, jiggers, seines, and gillnets are used in the coastal regions. Historically, gillnetting was the main method to catch cod in the coastal regions around Iceland, but longlines are becoming more common than gillnets due to increased market demand for fresh fish instead of salted cod. Gillnets are still used to catch cod in the winter and spring when these fish undergo spawning migrations. Fishing effort in Iceland's cod fishery is controlled under an individual transferrable quota (ITQ) system. The cod gillnet fishery, which is Marine Stewardship Council (MSC)-certified, has bycatch of marine mammals, predominantly harbor porpoises (*Phocoena phocoena*), while harbor seals (*Phoca vitulina*), grey seals (*Halichoerus grypus*), harp seals (*Pagophilus groenlandicus*), and white-beaked dolphins (*Lagenorhynchus albirostris*) are taken in smaller numbers (Pálsson et al. 2015). The cod fisheries have been identified as Export Fisheries by NOAA and therefore are subject to the Seafood Import Rule.

Gillnets are also used in Iceland to catch lumpsucker (*Cyclopterus lumpus*), commonly referred to as lumpfish. The lumpfish fishery uses large-mesh (267–292 mm) gillnets exclusively in shallow coastal waters of the southwest, west, and north of the country. The fishery targets lumpfish roe and is therefore highly seasonal, taking place during the spawning season (March–August), with the bulk of the fishing effort occurring in April and May (Kennedy et al. 2019). The fishery is effort-controlled, but it does not fall under the Icelandic ITQ system. Limits are placed on the total length of nets, total number of fishing days per boat, and total number of boats. Total catch is constrained by setting the total number of fishing days allowed for each boat. The fishery has bycatch, mostly of coastal seals but also harbor porpoises and seabirds because it uses large-mesh gillnets that are left in the water for several days (MFRI 2018*b*). Unsustainable levels of bycatch of harbor seals, grey seals, and black guillemots (*Cepphus grille*) led to the suspension and subsequent withdrawal of the fishery's MSC certification in 2019 (MSC 2019). There is limited exportation of lumpfish products to the US (~10 t out of an average total catch of ~4200 t in recent years; https://statice.is/), and it is uncertain whether that exportation will continue. In the initial implementation of the Seafood Import Rule, the lumpfish fishery was not identified as an Export Fishery.

The three species of marine mammals incidentally caught in the cod and lumpfish fisheries — harbor seals, grey seals, and harbor porpoises — have been identified as being of conservation concern in Iceland (NAMMCO 2018), due primarily to bycatch and hunting (seals). Local abundance of the two seal species has decreased substantially since monitoring was initiated in the 1980s (Þorbjörnsson et al. 2017; Granquist and Hauksson 2019*a*, 2019*b*).

The population of harbor seals, estimated from haul-out counts during the molting period, is close to 70% smaller than when surveys started around Iceland in 1980, with the last survey in 2018 resulting in an estimate of 9430 seals (Granquist and Hauksson 2019*b*; no measure of precision available). The grey seal population, based on pup production, was estimated to be 6270 animals, which is 30% smaller than when the first survey was conducted in 1982 (Granquist and Hauksson 2019*a*). Traditionally, both seal species were hunted for hides and meat, but this traditional use of the resource declined substantially in recent years. In addition, these seals were systematically culled through a bounty system introduced in 1982 in an effort to reduce the incidence of roundworm in commercial fish (Granquist and Hauksson 2019*a*). The bounty system for harbor seals ended around 1990, but continued at a low level for grey seals until at least 1998 (Erlingur Hauksson, personal communication). Although the systematic roundworm culling program was terminated in the 1990s, seal hunting–culling was subsidized by the fishing industry until 2018. In 2019, new legislation that banned all seal hunting in Iceland came into force. However,

Table 1. The population dynamic equations underlying the operating models.

Equation No.	Equation	Description
Population dynamics		
T1.1a	$N^s_{t+1,a} = \begin{cases} 0.5C_{t+1} & \text{if } a = 0 \\ S_{a-1}(N^s_{t,a-1} - M^s_{t,a-1}) & \text{if } 1 \le a < x \\ S_{x-1}(N^s_{t,x-1} - M^s_{t,x-1}) + S_x(N^s_{t,x} - M^s_{t,x}) & \text{if } a = x \end{cases}$	Basic population dynamics (continuous during conditioning)
T1.1b	$N^s_{t+1,a} = \begin{cases} \mathrm{B}(C_{t+1}, 0.5) & \text{if } a = 0 \\ \mathrm{B}(N^s_{t,a-1} - M^s_{t,a-1}, S_{a-1}) & \text{if } 1 \le a < x \\ \mathrm{B}(N^s_{t,x-1} - M^s_{t,x-1}, S_{x-1}) + \mathrm{B}(N^s_{t,x} - M^s_{t,x}, S_x) & \text{if } a = x \end{cases}$	Basic population dynamics (integer-based during the projection)
T1.2	$\mathrm{B}(z, p)$	Binomial distribution with parameters z and p
T1.3a	$C_t = b_t P_t$	Calf–pup production (continuous)
T1.3b	$C_t = \mathrm{B}(P_t, b_t)$	Calf–pup production (integer-based)
T1.4	$P_t = \sum_{a=a_p}^{x} N^{\mathrm{fem}}_{t,a}$	Breeding females
T1.5	$b_t = b_{\mathrm{eq}} \max\{0, 1 + (b_{\max}/b_{\mathrm{eq}} - 1)[1 - (N^{1+}_t/K^{1+})^{\theta}]\}$	Density-dependent birth rate
T1.6	$N^{1+}_t = \sum_s \sum_{a=1}^{x} N^s_{t,a}$	Number of animals aged 1 and older
T1.7	$M^s_{t,a} = \sum_{f=1}^{N_f} M^{s,f}_{t,a}$	Human-caused mortality by sex and age
T1.8a	$M^{s,f}_{t,a} = \phi^{s,f}_s \tilde{F}^f_t (N^s_{t,a} - \sum_{f'=1}^{f-1} M^{s,f'}_{t,a})$	Human-caused mortality by sex, age, and mortality-type (continuous)
T1.8b	$M^{s,f}_{t,a} = \mathrm{B}(N^s_{t,a} - \sum_{f'=1}^{f-1} M^{s,f'}_{t,a}, \phi^{s,f}_s \tilde{F}^f_t)$	Human-caused mortality by sex, age, and mortality-type (integer-based)
Conditioning		
T1.9a	$L_1 = \prod_{t \in t^*} \frac{1}{\sqrt{2\pi}\sigma^{1+}_t N^{1+,\mathrm{obs}}_t} e^{-\frac{1}{2(\sigma^{1+}_t)^2}(\ln N^{1+}_t - \ln N^{1+,\mathrm{obs}}_t)^2}$	Estimates of abundance
T1.9b	$L_2 = \prod_{t \in t^*} \frac{1}{\sqrt{2\pi}\sigma^{\mathrm{pup}}_t P^{\mathrm{obs}}_t} e^{-\frac{1}{2(\sigma^{\mathrm{pup}}_t)^2}[\ln(b_{\mathrm{eq}}P_t) - \ln P^{\mathrm{obs}}_t]^2}$	Pup production
Data generation		
T1.10	$\hat{N}_t = N^{1+}_t e^{\varepsilon_y - \sigma^2/2} \quad \varepsilon_y \sim \mathrm{N}(0, \sigma^2)$	Estimates of abundance

Note: Table 2 provides the definitions for the symbols.

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For harbor porpoise, there are indices of relative abundance, but only one estimate of absolute abundance, with a preliminary genetic kinship analysis suggesting an increase in stock abundance since the early 1990s (Víkingsson 2018). Harbor porpoises are not hunted systematically or regularly in Icelandic waters, and bycatch is therefore the main source of known anthropogenic mortality.

The species considered in this paper are thus subject to four sources of human-caused mortality: (*i*) bycatch in the Atlantic cod fishery, (*ii*) bycatch in the lumpfish fishery, (*iii*) deliberate removal of adult seals, and (*iv*) seal pup hunts.

Simulation testing and this study

The PBR formula and the way its parameters are defined for management in the USA were determined using simulations (Wade 1998) and specifically using a technique often referred to as management strategy evaluation (MSE; Bunnefeld et al. 2011; Punt et al. 2016). MSE involves developing (operating) models of the key elements of the management system (i.e., monitoring, decision making, and implementation) and projecting the populations in these operating models forward to determine how well management objectives might be met. MSE has been used to understand the behavior of the PBR approach (Brandon et al. 2017; Punt et al. 2018) and more generally to understand the behavior of conservation and management systems, including systems for marine mammal populations subject to harvesting and bycatch (e.g., IWC 2014, 2016, 2017*a*, 2017*b*; Punt and Donovan 2007; Punt et al. 2016). One aim of MSE is to develop a set of models (the operating models) to characterize the key sources of uncertainty and management strategies robust to those uncertainties. In the case of PBR, this includes uncertainty associated with productivity, the current size of the population in absolute terms and relative to management benchmarks such as the maximum net productivity level (MNPL), the precision and bias of survey-based estimates of population size, and the success of actual or prospective management regulations.

This paper compares various management strategies that aim to meet the requirements of the Seafood Import Rule for relevant fisheries in Iceland. It uses a set of operating models that explicitly represent several sources of human-caused mortality, unlike most previous MSE studies for marine mammal populations. Each of the sources is managed differently and not all pertain to fisheries subject to the Seafood Import Rule and therefore would not likely be subject to management changes related to rule compliance. Given the uncertainty regarding whether lumpfish will be exported to the USA in the future, the paper considers the implications of the lumpfish fishery being subject to and not being subject to the Seafood Import Rule.

Previous MSE studies related to PBR have either been based on generic models for cetaceans and pinnipeds (e.g., Wade 1998) or roughly tailored to the life histories of a range of marine mammals (Punt et al. 2018). This paper expands on that previous work by fitting the operating model to actual data for the species concerned, by representing multiple species that are affected by each source of mortality within a single operating model, and by exploring how management of a fishery's impact on one species is likely to affect conservation outcomes and fisheries for other species.

Table 2. The symbols included in the specification of the operating model.

Symbol	Description
C_t	No. of calves–pups at the start of year t
$\tilde{B}_t^f$	Mortality rate due to human-caused mortality for fully vulnerable animals that have survived mortality-types 1, 2, …, $f-1$
K^{1+}	Carrying capacity in terms of the number of animals aged 1 and older
$M_{t,a}^s$	Human-caused mortality of sex s and age a during year t
$M_{t,a}^{s,f}$	Human-caused mortality of sex s and age a by mortality-type f during year t
N_f	No. of fisheries
$\hat{N}_t$	Estimate of the number age-1+ animals at the start of year t
$N_{t,a}^s$	No. of animals of age a and sex s (male or female) at the start of year t
N_t^{1+}	No. of animals aged 1 and older at the start of year t
$N_t^{1+,\text{obs}}$	Observed number of animals aged 1 and older at the start of year t
$\tilde{N}_a^{\text{fem}}$	No. of females of age a at carrying capacity expressed as a proportion of the number calves–pups
P_t	No. of females that have reached the age of first parturition (a_p) at the start of year t
P_t^{obs}	Observer number of pups during year t
S_a	Survival rate for animals of age a
a_p	Age at first parturition
b_t	Birth rate during year t
b_{eq}	Birth rate when the population is at carrying capacity: $b_{\text{eq}} = (\sum_{a=a_p}^{s} \tilde{N}_a^{\text{fem}})^{-1}$
$b_{\max}$	Birth rate in the limit of zero population size
X	Plus-group age (values for the population dynamics parameters, including human-caused mortality rates, are the same from age x onwards)
$\phi_a^{s,f}$	Relative vulnerability of animals of age a and sex s to mortality-type f (the most vulnerable class has $\phi_a^{s,f} = 1$, and it is to this class that $\tilde{B}_t^f$ pertains)
θ	Shape parameter, which determines where MNPL occurs relative to carrying capacity
σ	The standard error of the observation errors (i.e., $\sigma^2 = \ln(1 + \text{CV}_N^2)$), where CV_N is the coefficient of variation about the true abundance
σ_t^{1+}	Standard error of the logarithm of $N_t^{1+,\text{obs}}$ (0.45 for harbor porpoise, and $\sqrt{0.1^2 + \Omega}$ where Ω is the extent of additional variance for the two seal species)
σ_t^{pup}	Standard error of the logarithm of P_t^{obs}
Ω	Additional variance (harbor and grey seals)

Methods

Overview

A MSE involves four steps: (*i*) identifying management objectives and their quantification using performance metrics, (*ii*) developing and parameterizing a set of operating models, (*iii*) identifying candidate management strategies (in this paper, decisions regarding which sectors to manage and how, as well as the quality of the data available on which management decisions would be based), and (*iv*) projecting the populations in operating models forward for each management strategy and computing the performance metrics. The following sections outline (1) the operating models and how they are fitted to the available data, (2) the scenarios considered, which relate to the management strategies and how the operating models are specified, and (3) the performance metrics that quantify the management objectives of the MMPA (recovery of mammal populations to MNPL) and those of countries whose fisheries are subject to the Seafood Import Rule.

Operating models

Each operating model is a set of single-area, age- and sex-structured population dynamics models, one each for harbor porpoises, harbor seals, and grey seals. The operating models are deterministic and continuous for the years before the projections under the management strategies start and are integer-based for the projections, where the numbers of births and deaths are modeled as binomial random variables (eqs. T1.1a, T1.b; Table 1; for definitions of all symbols, refer to Table 2). The assumption of deterministic and continuous dynamics is made for the period before the projections start to facilitate conditioning of the operating models[1], although it is necessary to allow for demographic stochasticity and represent the population by age and sex as integers in the future to more fully capture uncertainty. The number of calves or pups produced each year depends on the number of females that have reached the age of first parturition (eq. T1.4) and a birth rate that is density-dependent, with the extent of density dependence being a function of the abundance, relative to carrying capacity (K), of animals aged 1 and older (eq. T1.5).

Each population in an operating model is assumed to have a stable age structure at the start of the first year considered (1950), given an assumed bycatch mortality rate that is the same for all animals aged 1 and older. That bycatch mortality rate and hence the number of animals by age and sex at the start of 1950 are computed based on carrying capacity and the number of age-1+ animals relative to that at carrying capacity (IWC 2017*b*). There are no data on the age and sex of the removals or on abundance. The model nevertheless keeps track of the population by age and sex given the assumptions regarding the initial conditions along with the equations defining the age- and sex-structured model.

Each operating model assumes that there are four sources of human-caused mortality: (*i*) bycatch mortality in the Atlantic cod fishery, (*ii*) bycatch mortality in the lumpfish fishery, (*iii*) deliberate removal of age-1+ seals, and (*iv*) hunting for seal pups (see online Supplementary Fig. 1[2] for the time series of removals by species). Total human-caused mortality (eq. T1.7) is hence the sum

[1]Conditioning is the process of assigning the values to the parameters of the operating model (Punt et al. 2016).

[2]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2019-0386.

Table 3. The base-case prespecified parameters of the population dynamics model and the prior distributions for the estimated parameters.

Parameter	Harbor porpoise	Harbor seal	Grey seal
Prespecified parameters			
MNPL/K[a]	0.6	0.6	0.6
S_{adult}	0.920[b]	0.929[b,c]	0.929[d]
CV of bycatch rate	0.3	0.3	0.3
Age-at-maturity	4[e]	5[e]	6[f]
Estimated parameters			
MSYR_{1+}[g]	U[0.01, 0.12]	U[0.02, 0.12]	U[0.02, 0.12]
Maximum birth rate[h]	Set to 0.98	U[0.5, 2.0]	U[0.5, 2.0]
N_{1950}/K[i]	U[0.7, 0.9]	U[0.7, 0.9]	U[0.7, 0.9]
Current abundance	43 179 (CV = 0.45) (2007)[j]	7652 (CV = 0.1) (2016)[k]	1452 (CV = 0.1) (2017)[l]
Additional variance[g]	Absolute estimate of abundance: set to 0 Close kin estimates: U[0, 0.5] Sightings rates: U[0, 1.5]	U[0, 0.7]	U[0, 0.5]

Note: Some of the values are varied in the alternative operating models.
[a]Taylor and DeMaster (1993).
[b]J. Moore (unpublished data) estimate following methodology of Dillingham et al. (2016).
[c]Hastings et al. (2012).
[d]Harwood and Prime (1978).
[e]NMFS (2018*b*).
[f]Hammill and Gosselin (1995).
[g]Priors to set a wide enough range that the posterior is covered.
[h]Ólafsdóttir et al. (2003).
[i]Assumed (sensitivity is explored to an alternative range).
[j]Gilles et al. (2011).
[k]Þorbjörnsson et al. (2017).
[l]Granquist and Hauksson (2019*a*; assumed to pertain to pups before density dependence).

of four source-specific mortalities. For computational ease, the sources are assumed to remove individuals from the modelled populations sequentially; specifically, cod bycatch mortality occurs first, followed by lumpfish bycatch mortality, etc. (eq. T1.8). The relative vulnerability[3] to each source of mortality by sex and age, $\phi_a^{s,f}$, for the first three sources is assumed to be uniform over all age-1+ animals, while only pups are assumed to be vulnerable to the pup hunt.

Each operating model is parameterized for the three species in terms of four demographic parameters: (*i*) MSYR_{1+}, the bycatch rate for animals age-1+ and older that would reduce the population to the size at which maximum production would be achieved (equivalent to the rate of increase when the population is at its MNPL); (*ii*) the maximum birth rate; (*iii*) the number of age-1+ animals in 1950 relative to the carrying capacity; and (*iv*) a measure of current abundance (either in terms of age-1+ numbers or numbers of calves or pups born annually, depending on the data source; Supplementary Table S1[2]). Natural survival is assumed to be the same for all age-1+ animals (S_{1+}) and to differ from that of age-0 animals (S_0). It is possible to compute S_0 and the two parameters of the density dependence function (eq. T1.5) given MSYR_{1+}, the age-at-maturity, the maximum birth rate, S_{1+}, and MNPL/K (Punt 1999). Parameter combinations for which the age-0 survival rate (which depends on MSYR_{1+} and the maximum birth rate) exceeds the survival rate for age-1+ animals are rejected as biologically implausible.

The likelihood functions for the estimates of age-0+ abundance (harbor seals), age-1+ abundance (harbor porpoises), and the pup production (grey seals) (eq. T1.9) include an (estimable) additional variance parameter, Ω. The default coefficients of variation (CVs) for these abundance estimates, which are 0.1 (Supplementary Table 1[2]), underestimate uncertainty, and there is no way to estimate sampling error for these estimates directly. There is no additional variance for the absolute abundance estimate for harbor porpoises because the abundance estimate uncertainty measures are consistent with the model fit. A prior is not assigned to carrying capacity. Rather, K is solved for, given the remaining parameters, using the backwards method of Butterworth and Punt (1995) and Punt (2019). That method involves applying a root-finding method to select K, such that if the population is projected from a generated relative abundance in 1950 (i.e., N_{1950}/K) to the present, then the projected population size equals the value generated for current abundance.

Each operating model is conditioned (distributions assigned to the parameters) using a Bayesian estimation approach based on the sample–importance–resample (SIR) algorithm (Rubin 1987; Van Dijk et al. 1987). The SIR algorithm is implemented separately for each species by drawing parameter vectors from priors and computing posteriors until the posterior is represented by 100 unique parameter vectors (1000 for summarizing the posteriors). Table 3 lists the model parameters that are prespecified, the priors assumed for the estimable parameters, and the sources for the prespecified parameters and the priors. The data available to update the prior distributions differ among species and the population component to which they are linked (Supplementary Table 1[2]), and the indices are assumed to be independent and lognormally distributed. The pup production for grey seals is assumed to relate to pups immediately after birth and before density dependence (i.e., $b_{\text{eq}}P_t$).

Each evaluation of a management strategy is based on 1000 replicate projections (i.e., 10 projections for each of 100 parameter vectors sampled from the posterior). The random numbers used to determine the future survey estimates of abundance are the same for each evaluated management strategy but, owing to the stochastic nature of the projections, the random numbers governing the population dynamics are not the same for each management strategy, which likely leads to small differences among the results for the various management strategies.

Within the MSE, future estimates of abundance are assumed to become available every 4 years starting in 2021, and it is assumed

[3]In the sense that the maximum value over ages and sexes is 1.

Table 4. The alternative operating models.

Operating model	Description and rationale
Base-case	See text
1	$N_{1950}/K \sim$ U[0.5, 0.7]; more conservative initial depletion distribution
2	$MSYR_{1+}$ is set to 0.02 for harbor porpoises and 0.06 for seals; set to values close to US defaults
3	MNPL/K = 0.5; set the value used in the simulations by Wade (1998)
4	CV of bycatch rate = 0.2; the base-case value is arbitrary; this value is lower
5	CV of bycatch rate = 0.4; the base-case value is arbitrary; this value is higher
6	Ignore the two kinship-based estimates of abundance for harbor porpoise; these estimates may be driving the apparent increase in abundance
7	90% of the seal bycatch mortalities are juveniles of age-0

that it takes 2 years to analyze the survey data before those estimates are available to be used for management purposes. The sampling error for the estimates of abundance is assumed to be lognormal (eq. T1.10). The additional variance, Ω, is an estimated parameter (Table 3) and hence differs among draws from the posterior. The abundance estimates for the years prior to the start of the projection period are set to the historical values (Supplementary Table 1[2]). The estimates of total abundance (which are required for computing PBR) for grey seals are based on multiplying estimated pup production by four (Granquist and Hauksson 2019*a*). Thus, within the MSE, the expected values for the generated abundance estimates for grey seals are based on multiplying the number of pups (before density dependence) by four and hence the estimated population size used in the PBR formula refers to age-1+ animals. The annual mortalities are assumed to be estimated subject to lognormal variation with a CV of 0.3.

Data for conditioning

Abundance of the two seal species is monitored using estimates of pup production (grey seals) and haul-out counts (harbor seals) (Þorbjörnsson et al. 2017; Granquist and Hauksson 2019*a*, 2019*b*). Although cetacean sighting surveys have been conducted regularly in Icelandic waters since 1986, these have been designed for whales, and estimates of harbor porpoise are likely biased downward to an unknown extent. While the 2007 aerial survey still had the common minke whale (*Balaenoptera acutorostrata*) as the primary target species, some adjustments were made to improve estimation of the abundance of harbor porpoises (Gilles et al. 2011). Consequently, the 2007 estimate is considered the most reliable for Icelandic coastal waters and is assumed to be an estimate of absolute abundance in contrast with the other estimates of abundance, which are taken to provide only information on trends. Data on sighting rates in aerial surveys are available for the last 30 years (1986–2016), along with indices of abundance for 2017 and 2018 based on preliminary kinship analyses (Víkingsson 2018).

Scenarios

Scenarios relate to (*i*) some of the prespecified aspects of the operating model (which are not controllable by management; i.e., the various alternative operating models) and (*ii*) aspects of the management system (which are controllable by management; i.e., the alternative management strategies). The operating models (Table 4) explore the effects of the true situation differing from the base-case operating model, which is based on the assumptions and parameter values in Table 3. The factors in Table 4 examine sensitivity to the value of MNPL/K, the variation in future bycatch rates about their expected values, and prespecifying $MSYR_{1+}$ to 0.02 for the harbor porpoise and 0.06 for the two seal species (i.e., half the maximum rates of increase assumed in the calculations by Wade 1998). The assumption that $MSYR_{1+}$ equals 0.02 for the harbor porpoise is very conservative given data on observed rates of increase for some previously depleted populations (K. Forney, unpublished data) and predictions from allometric theory following the methods of Moore 2015 (also see Moore et al. 2018), but it is included here to explore the robustness of the results for harbor porpoises off Iceland for which the relative abundance estimates are fairly imprecise and variable. The sixth alternative operating model involves excluding the estimates of abundance based on kinship analysis because the sample sizes are small (NAMMCO 2019), and the final operating model assumes that 90% of the bycatch of both seal species in the Atlantic cod and lumpfish fisheries are juveniles of age-0. This final alternative operating model is used because evidence suggests that a considerable proportion of the animals bycaught in these fisheries are younger than age-1. The operating model scenarios involve applying the SIR algorithm to create a set of operating model parameters specific to the scenarios.

Management regulations in the simulations of this paper (and hence bycatch rates by source of mortality) were updated every 5 years based on application of the management strategy. Under the Seafood Import Rule, it is only necessary to manage fisheries that export to the USA. For the purposes of this paper, these are the cod gillnet fishery and, perhaps, the lumpfish fishery. Thus, the reference-case projections assume that the expected bycatch mortality rate due to the cod (and lumpfish) fisheries will change in response to monitoring, with the realized bycatch mortality rate modelled as a beta random variate with mean set to an expected bycatch mortality rate and a CV of 0.3. (This mimics the assumptions of Wade (1998), who assumed that the extent to which removals could be managed could be modelled by a normal distribution with a CV of 0.3.) The annual bycatch mortality rates for the remaining sources of human-caused mortality are sampled from beta distributions with means set to the average bycatch mortality rates by source for the 5 years prior to first application of the management system and a CV of 0.3.

The reference-case management strategy is based on computing the PBR for each species where time management regulations are updated. The PBR is calculated by applying a control rule that is the product of three parameters: (*i*) a minimum estimate of abundance "that provides reasonable assurance that the stock size is equal to or greater than the estimate" (N_{MIN}); (*ii*) one-half of the maximum intrinsic rate of population growth (0.50 R_{MAX}); and (*iii*) a recovery factor (F_R) between 0.1 and 1.0 (Wade 1998):

$$\text{PBR} = N_{MIN}\, 0.50\, R_{MAX}\, F_R \tag{1}$$

Within the USA, the default values of parameters of the PBR formula are R_{MAX} = 0.04 for cetaceans and 0.12 for pinnipeds, so R_{MAX} is set to 0.04 for the harbor porpoise and 0.12 for harbor and grey seals, N_{MIN} = the lower 20th percentile of the (lognormal) distribution for recent abundance estimates, and F_R is selected depending on the status of the stock (Wade 1998). Harbor and grey seals are currently (2018) assessed to be below MNPL, so F_R is set to 0.5 for these species. It is set to 1 for the harbor porpoise, which is estimated to be above MNPL with more than 0.5 probability for most of the operating models (see below).

The PBR from eq. 1 is compared with the average level of mortality due to human causes over the preceding 5 years and the

Table 5. Management strategies.

Scenario	Description
Reference	PBRs are computed and effort levels in the cod and lumpfish fisheries are reduced by the ratio of PBR to recent average human-caused mortalities separately by species (F_R = 1 for harbor porpoises; 0.5 for the other species)
A	No updated management arrangements
B	Zero human-caused mortality for all fisheries
C	Cod and lumpfish effort is reduced by the maximum inferred rate of bycatch reduction among species
D	PBRs are computed and effort for the cod fishery is reduced by the ratio of PBR to recent average human-caused mortalities separately by species
E	Cod effort is reduced by the maximum inferred rate of bycatch mortality rate reduction
F	All hunting or removal mortality is eliminated (but there is future bycatch mortality at current levels)
G	No future bycatch mortality (but there is future hunting or removal mortality)
H	As for the reference case, but F_R = 0.5 for all species
I	As for the reference case, no future additional variance; lower CV for harbor porpoise (0.2)
J	All sources of human-caused mortality are managed (species-specific changes in mortality rates by source)
K	All sources of human-caused mortality are managed (species-independent change in mortality rates by source)
L	As for strategy J, but the rate of human-caused mortality cannot increase
M	As for the reference case, but R_{MAX} is assumed 0.09 for harbor porpoises when calculating PBR

bycatch mortality rate (from the cod (and lumpfish) fishery) changes in proportion to this ratio:

$$\hat{B}_y^f = \bar{B}_{y-5:y-1}^f \mathrm{PBR}_y \Big/ \left(\hat{\bar{M}}_{y-5:y-1}^{\mathrm{fem}} + \hat{\bar{M}}_{y-5:y-1}^{\mathrm{mal}}\right) \quad (2)$$

where $\hat{B}_y^f$ is the expected bycatch mortality rate for the fishery f (cod or lumpfish) in year y, $\bar{B}_{y-5:y-1}^f$ is the average bycatch mortality rate in fishery f for the 5 years prior to year y, PBR_y is the PBR computed for year y, and $\hat{\bar{M}}_{y-5,y-1}^s$ is the estimate of average mortality of animals of sex s due to all sources of human-caused mortality for the 5 years prior to year y. The reference-case projections assume that management is such that the adjustments to cod (or lumpfish) fishery effort can be made independently for each species.

Table 5 lists the alternative management strategies, which examine, inter alia:

- managing more (or all) sources of human-caused mortality;
- computing the PBR for each marine mammal species separately using eq. 2 and changing the effort for the cod and lumpfish fisheries based on the minimum ratio (over species) of PBR to average catch;
- changing the CVs of the surveys when applying PBR and hence developing management regulations;
- allowing for decreases in bycatch mortality rates but not subsequent increases;
- assuming a higher value for R_{MAX} when calculating the PBR for harbor porpoises given the results of the base-case analysis.

Performance metrics

There are two performance metrics:

- The probability of the number of age-1+ animals exceeding MNPL. This probability is computed at the start of the projection period (2018), after 16–20 years, and after 96–100 years. The probability is computed based on an average over a 5-year period to reduce the effects of demographic stochasticity. The choice of 100 years is based on Wade (1998), who selected the values of the PBR formula based on 100-year projections.
- The median (over the 100 projections) of the ratio of the bycatch mortality rate in the cod and lumpfish fisheries after 16–20 years and 96–100 years to the average bycatch mortality rates for these fisheries during 2013–2017.

The first performance metric pertains to the rate of recovery of the population. Wade (1998) identified a performance "standard" of a 95% probability of recovery to MNPL after 100 years for a population initially at 30% of its carrying capacity with an MNPL of 0.5K. This performance standard is used to guide interpretation of results, but given that the populations here are not starting at 30% of K (i.e., 0.6MNPL), it cannot be used as a hard standard for recovery rate. The second performance metric pertains to the reduction in fishing intensity following implementation.

Results

Conditioning the operating model

The SIR algorithm generated 1000 unique parameter vectors for each species (see Supplementary Table 2[2] for a numerical summary of the posteriors). Figure 1 shows the estimated time trajectories of age-1+ abundance (posterior medians and 50% and 95% intervals), along with the abundance estimates used for conditioning. The data for harbor seals pertain to age-0+ abundance, while those for grey seals pertain to pup production (i.e., the model predictions for grey seals are based on numbers of pups prior to density dependence). The model fits the data very well, except for the sighting rates for harbor porpoises (Fig. 1; top right panel), although these estimates display considerable among-year variation, which would be consistent with the Icelandic continental shelf waters hosting only a part of a wider population (Pike et al. 2009). The extent of additional variance is such that these data provide very little information on population trend.

Figure 2 summarizes the outcomes of the Bayesian analyses in terms of posteriors for MSYR_{1+}, additional variance, and initial (1950) and current (2019) relative abundance. It also shows the posterior for the abundance in the reference year (the year for which a prior is imposed on abundance: 2007, 2016, and 2017 for harbor porpoises, harbor seals, and grey seals, respectively; Table 3), along with the assumed prior distribution for this abundance. There are no estimates of historical population size except for the abundance estimates (which are used when fitting the model), precluding using independent data to validate the model. However, the posterior median estimates of pre-exploitation size (K) and size in 1980 for harbor seals are similar to the estimates obtained by Hauksson and Einarsson (2010) (e.g., 1980 abundance 33 000 (90% CI: 26 000–44 000)) based on a different model and estimation framework.

The prior for MSYR_{1+} is updated substantially for all three species. The median posterior for MSYR_{1+} for grey seals is close to that expected given the default values for R_{MAX} assumed by Wade (1998) (i.e., 0.5R_{MAX}), but the posteriors for MSYR_{1+} for harbor porpoises and harbor seals are more optimistic. The higher estimated productivity for harbor porpoises compared with cetaceans generally is perhaps not unexpected given harbor porpoises have reduced longevity, earlier maturation, and higher per capita reproductive rates compared with other odontocetes (Read and

Fig. 1. Time series of estimated age-1+ abundance (left column) and, where appropriate, fits to time series of abundance data for the base-case operating model (middle column). The dark lines are posterior medians, the dark shading covers the 50% probability intervals, and the light shading covers the 90% probability intervals. The sampling intervals for the abundance indices account for the default CV as well as the median additional variance. The *y* axes are scaled to the data for the two relative abundance indices for the harbor porpoise (top center and top right panels).

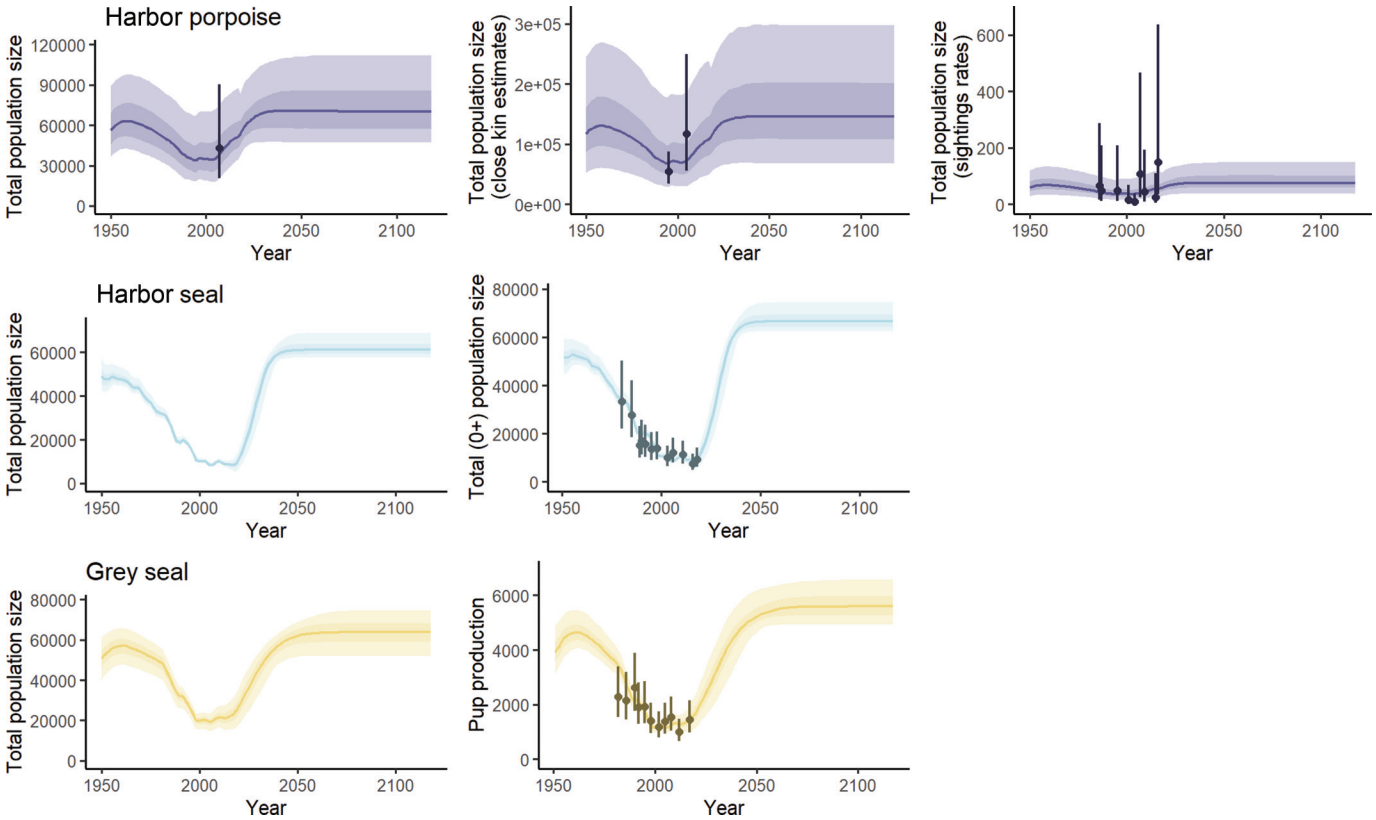


Fig. 2. Posterior distributions for the estimated parameters, the posterior for the abundance in the reference year (the year for which a prior is imposed on abundance: 2007, 2016, and 2017 for harbor porpoises, harbor seals, and grey seals, respectively; Table 3), along with the assumed prior distribution for this abundance (second to last column) and the posterior distribution for the depletion at the start of the projection period (depletion is the ratio of age-1+ numbers in a given year to the numbers at carrying capacity).

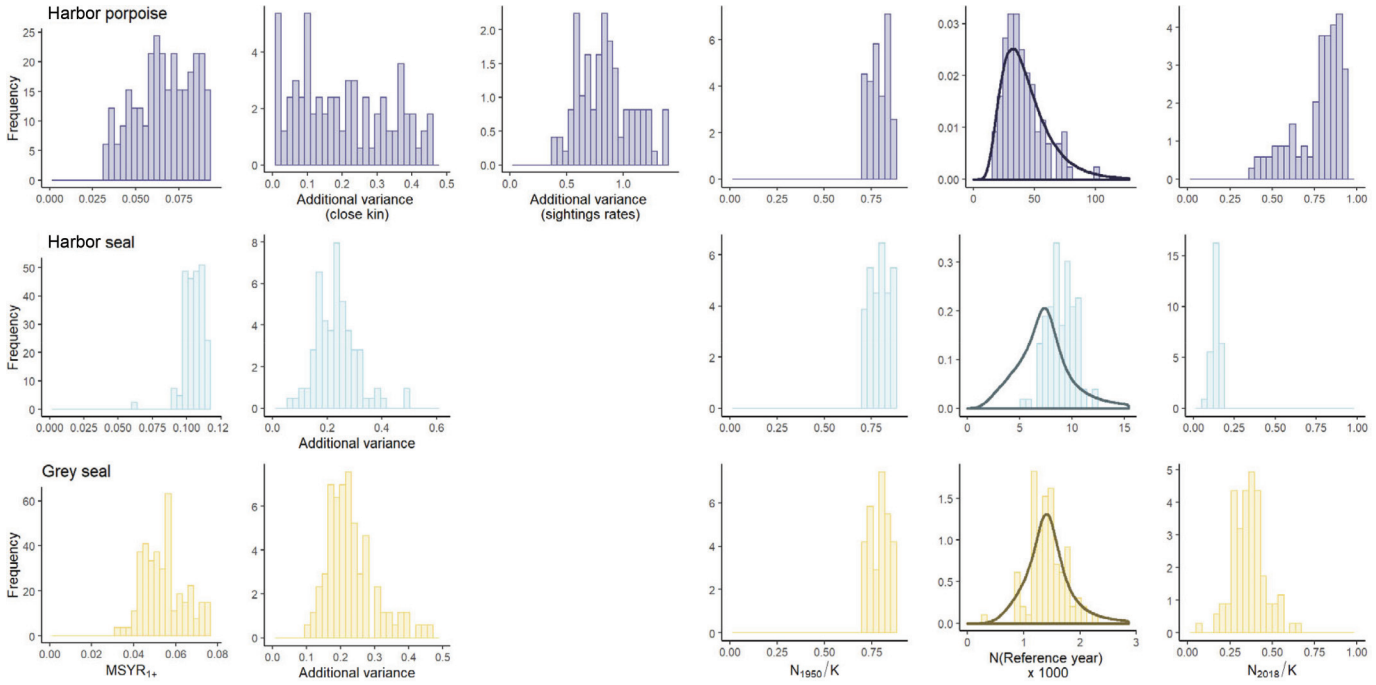
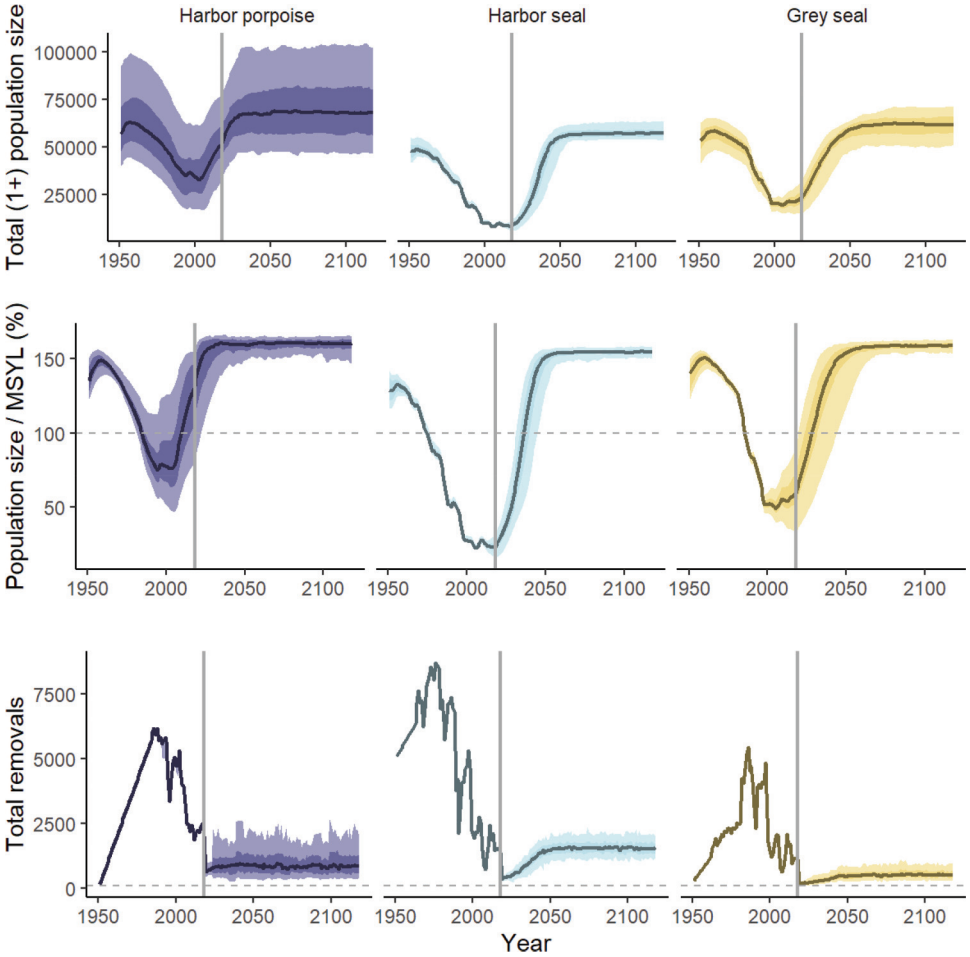


Fig. 3. Distributions (dark lines are medians; dark shading covers the 50% intervals; light shading covers the 90% intervals) for historical (1950–2018) and projected age-1+ abundance (in absolute terms and relative to MNPL) and mortalities due to all sources for the base-case operating model and the reference-case management strategy. The grey vertical line indicates the start of the projection period (2018).



Hohn 1995). Sensitivity analyses examined the management consequences of setting $MSYR_{1+}$ in the operating model rather than estimating it (Table 4). The posteriors for additional variance (expressed as a CV) indicate that the "default" CV of 0.1 underestimates the true extent of sampling error for the two seal species and the two relative abundance indices for harbor porpoises. In contrast with $MSYR_{1+}$ and the additional variance parameter, the priors for initial relative abundance and the abundance in the reference year (except for harbor seals) are not updated substantially, and the entire prior ranges are well represented in the posterior.

The posterior distributions for depletion in 2018 indicate that harbor porpoises are likely above MNPL (and hence not necessarily in need of additional management arrangements), while grey seals and particularly harbor seals are well below MNPL.

Projection results — reference-case analysis

Figure 3 shows distributions for historical (1950–2018) and projected total age-1+ abundance (in absolute terms and relative to MNPL) and mortality due to all sources for the base-case operating model and the reference-case management strategy. Figures 4 and 5 show the distributions for human-caused mortality and bycatch mortality rate by source. The harbor porpoise population is above MNPL in 2018 and continues to increase thereafter, with a probability of being above MNPL of ~100% within 20 years (Table 6, row "Reference"). Grey and harbor seals also recover over the 100-year projection period.

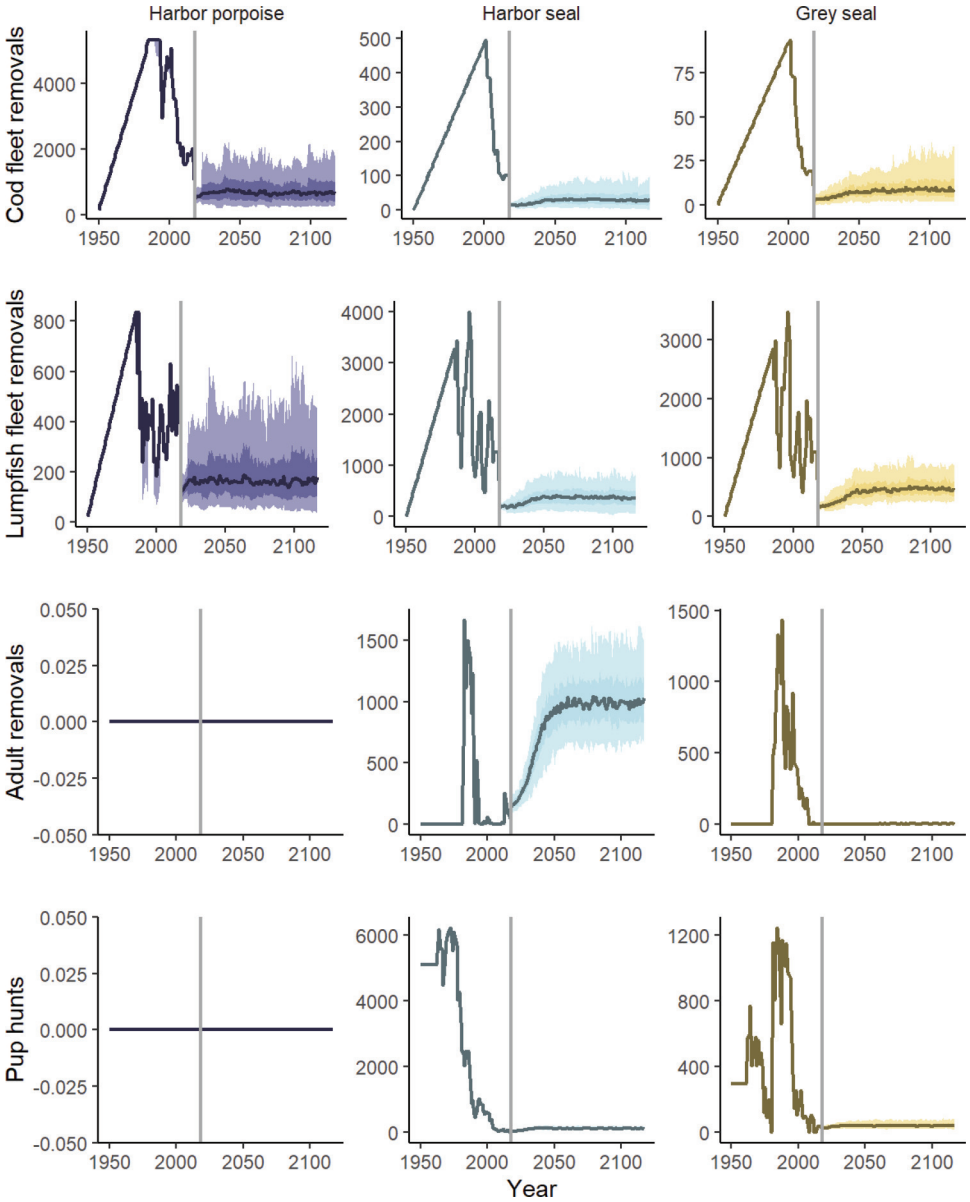
Fishing intensity in the cod and lumpfish fisheries is predicted to decline over time for all three species because the bycatch mortality rates for these fisheries are reduced to 24%–27% (harbor porpoises), 4%–5% (harbor seals), and 12%–16% (grey seals) of their current level. In contrast, the rates of removal by hunting of age-1+ animals and of hunting of pups are constant (albeit fairly low) for the reference-case management strategy (Fig. 5). For this operating model, an increase in deaths of harbor seals due to these sources of mortality, in conjunction with increasing abundance, is implied given the assumption of continuing constant rates of mortality (Fig. 4).

Projection results — alternative management strategies

Table 6 summarizes the performance metrics for the alternative management strategies. Not changing management arrangements (Table 6, row A) has little effect on the rate of recovery for harbor porpoises, which is not unexpected given harbor porpoises are predicted to have been recovering under current bycatch rates (Fig. 3). Harbor porpoises were likely depleted as gillnet fishing effort increased during the latter half of the 20th century, but management changes to the fishery and associated reductions in effort have supported a likely recovery. In contrast, grey and (particularly) harbor seals are not above MNPL after 100 years. There is some recovery of grey seals but not at the same rate as the reference management strategy (Fig. 6).

Eliminating all sources of human-caused mortality (Table 6, row B) leads, as expected, to high rates of recovery, with all populations

Fig. 4. Distributions (dark lines are medians; dark shading covers the 50% intervals; light shading covers the 90% intervals) for historical (1950–2018) and projected mortalities by marine mammal species (columns) for each of the sources of human-caused mortality (rows) for the base-case operating model and the reference-case management strategy. The grey vertical line indicates the start of the projection period (2018).

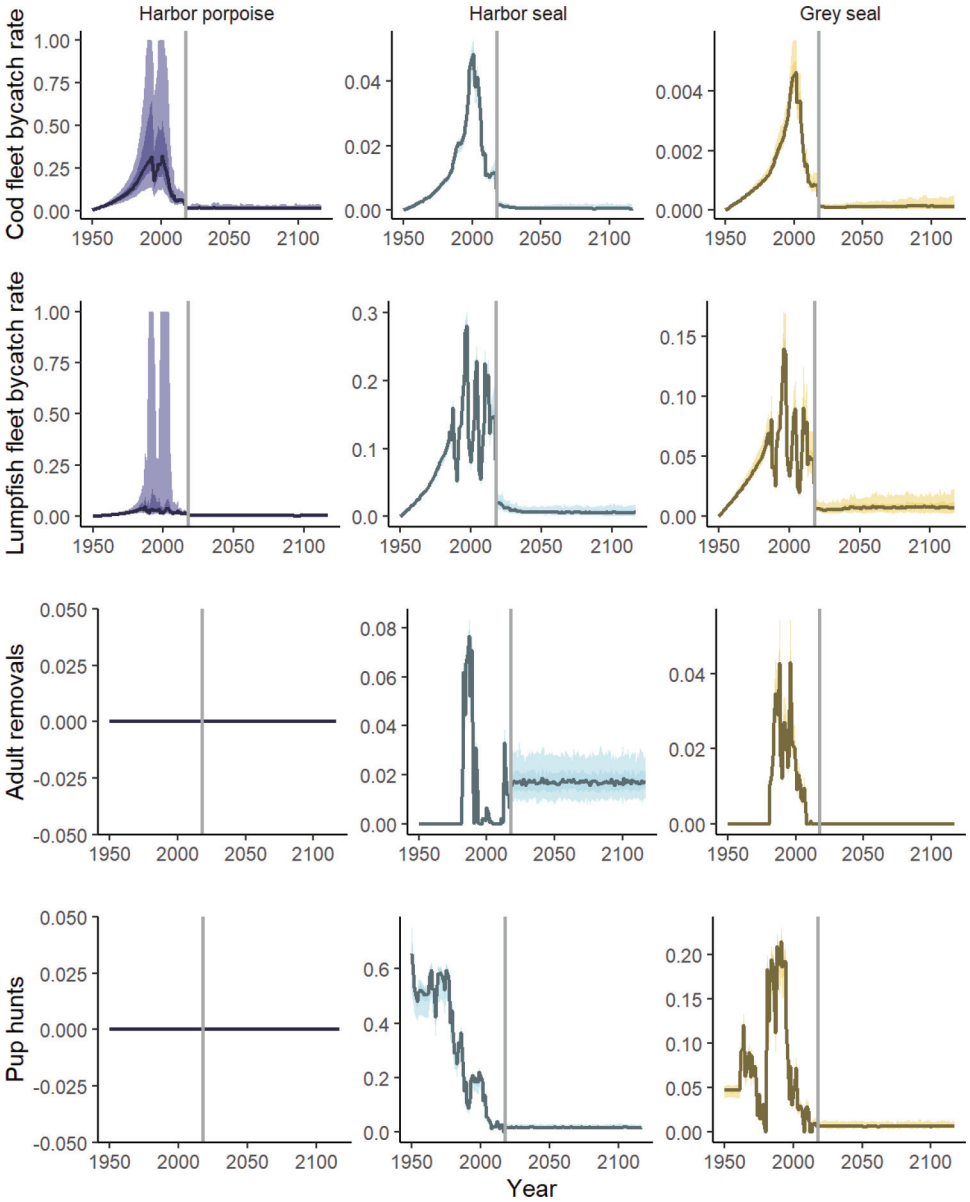


at (or close to) carrying capacity after 100 years. Managing the cod and lumpfish fisheries based on reducing effort by the maximum reductions by species, which is required for the recovery of harbor seals, leads to a slightly greater rate of recovery for the harbor seals, but much greater reductions in fishing intensities as inferred from changes in bycatch rates (Table 6, row C). Managing only the cod fishery (under the assumption that lumpfish will no longer be exported to the US) leads to markedly lower rates of recovery for the two seal species (Table 6, rows D and E). This is not unexpected given that the lumpfish fishery is the major source of bycatch for the two seals.

Eliminating hunting and sources of mortality other than bycatch (Table 6, row F) allows harbor porpoises (which are not hunted) to continue to recover but not the seals. In contrast, eliminating bycatch mortality but not other sources of mortality (Table 6, row G) nearly achieves the same rates of recovery as eliminating all sources of human-caused mortality by the end of the 100-year period. Changing F_R for harbor porpoises or improving the precision of the indices of abundance (management strategies H and I) has minimal impacts on the results compared with those for the reference-case management strategy.

Managing all sources of human-caused mortality rather than just bycatch in the cod and lumpfish fisheries (Table 6, rows I, J, and K) leads to faster rates of recovery for harbor seals over the first 15–20 years of the projection period, indicating that the non-bycatch sources of mortality are hindering recovery to some extent — although bycatch in the lumpfish fishery is clearly the major source of mortality (Fig. 5). Not allowing mortalities due to bycatch to increase over time (which would be expected if mortalities equal PBR on average and populations are increasing; e.g., Figure 3) leads to faster rates of recovery (Table 6, row L), but at the cost of needing stronger restrictions on the cod and lumpfish fisheries in the future to force bycatch mortality rates to drop so as to compensate for the increasing population sizes.

Fig. 5. Distributions (dark lines are medians; dark shading covers the 50% intervals; light shading covers the 90% intervals) for historical (1950–2018) and projected mortality rate by marine mammal species (columns) for each of the sources of human-caused mortality (rows) for the base-case operating model and the reference-case management strategy. The grey vertical line indicates the start of the projection period (2018).



Assuming R_{MAX} = 0.09 for the harbor porpoises has little impact on recovery rates for harbor porpoise, but much lower impacts on the fishing intensity for the fisheries (Table 6, row M).

Projection results — alternative operating models

Table 7 lists the performance metrics for six management strategies (the reference management strategy, no changes in management (A), two strategies in which only bycatch in the cod fishery is managed (D and E), management strategy L, and management strategy M) for the base-case operating model and five of the seven alternative operating models (Table 4; see Supplementary Table 3[2] for the results for operating models 4 and 5). The five management strategies other than the reference management strategy were selected because they led to the broadest set of outcomes and captured a consequential management uncertainty, which is whether the lumpfish fishery will be managed to reduce bycatch. Supplementary Figs. S2–S6[2] show the diagnostics related to model fits.

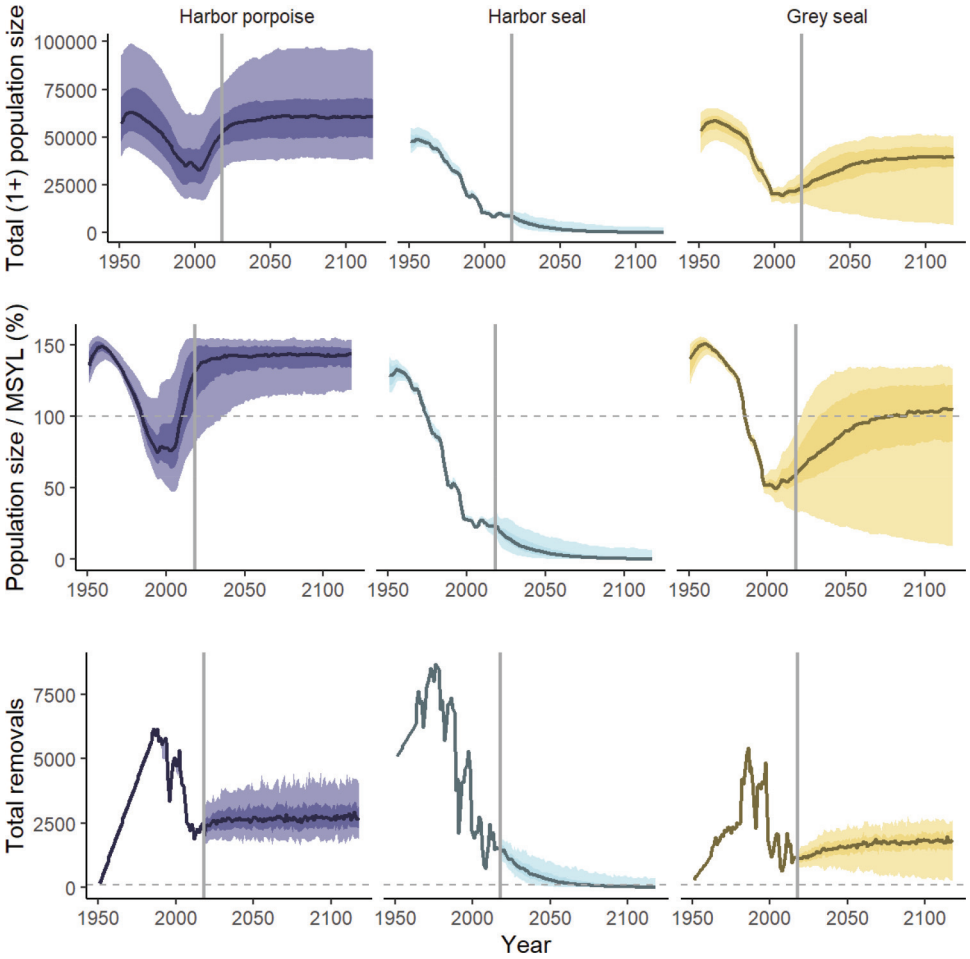
The results when the prior for initial (1950) depletion is set to U[0.5, 0.7] are similar to, but somewhat less optimistic than, those for the base-case operating model. The lack of a substantial effect occurs because of rebuilding during 1950–1970 when human-caused mortality was relatively low (Supplementary Figs. S1 and S2[2]). Setting $MSYR_{1+}$ to 0.02 for harbor porpoises and 0.06 for the seal species leads to a better fit to the 2007 abundance estimate for harbor porpoises and an inability to mimic the decline in the abundance estimates for harbor seals (Supplementary Fig. S3[2]). The probability of harbor porpoises currently being above MNPL is lower for this operating model (0.02 compared with 0.82 for the base-case operating model). However, the reference management strategy allows all three species to recover to MNPL within 95–100 years, although the probability of recovery for harbor seals is

Table 6. Values for the performance metrics for the base-case operating model and 14 management strategies.

Management strategy	Probability of exceeding MNPL (%)						Cod effort			Lumpfish effort			Cod effort			Lumpfish effort		
	Years 15–20			Years 95–100			Years 15–20						Years 95–100					
	HP	HS	GS	HP	HS	GS	HP	HS	GS	HP	HS	GS	HP	HS	GS	HP	HS	GS
Reference	99.8	68.0	91.8	100.0	100.0	100.0	0.27	0.05	0.12	0.26	0.05	0.12	0.25	0.04	0.15	0.24	0.04	0.16
A	95.9	0.0	32.6	99.0	0.0	54.5	1.00	0.99	1.00	0.99	0.99	0.99	1.00	1.01	0.99	1.00	0.99	0.99
B	100.0	96.0	93.0	100.0	100.0	100.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
C	100.0	69.7	93.0	100.0	100.0	100.0	0.05	0.05	0.05	0.05	0.05	0.05	0.04	0.04	0.04	0.04	0.04	0.04
D	99.0	0.0	33.0	100.0	0.4	56.6	0.12	0.00	0.00	0.99	0.99	0.99	0.06	0.00	0.00	1.00	0.99	0.99
E	99.0	0.0	33.0	100.0	0.4	57.5	0.00	0.00	0.00	0.99	0.99	0.99	0.00	0.00	0.00	0.99	0.99	0.99
F	95.7	0.0	32.0	99.0	1.0	56.2	0.99	0.99	0.99	0.99	0.99	0.99	0.99	0.99	1.00	0.99	0.99	0.99
G	100.0	85.7	93.0	100.0	100.0	100.0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
H	100.0	68.0	91.8	100.0	100.0	100.0	0.13	0.05	0.12	0.13	0.05	0.12	0.12	0.04	0.15	0.12	0.04	0.16
I	99.6	68.4	92.0	100.0	100.0	100.0	0.35	0.05	0.12	0.34	0.05	0.12	0.33	0.04	0.16	0.31	0.04	0.17
J	99.8	79.1	91.4	100.0	100.0	100.0	0.27	0.14	0.14	0.26	0.14	0.14	0.25	0.14	0.16	0.24	0.14	0.17
K	100.0	84.0	92.5	100.0	100.0	100.0	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.11	0.10	0.11	0.11	0.11
L	99.9	83.7	92.7	100.0	100.0	100.0	0.18	0.11	0.10	0.18	0.11	0.10	0.10	0.08	0.07	0.09	0.08	0.07
M	98.8	68.0	91.8	99.1	100.0	100.0	0.62	0.05	0.12	0.60	0.05	0.12	0.58	0.04	0.15	0.57	0.04	0.16

Note: HP, harbor porpoise; HS, harbor seal; GS, grey seal. The probabilities of being above MNPL at the start of the projection period are 82%, 0%, and 1%, respectively, for harbor porpoises, harbor seals, and grey seals.

Fig. 6. Distributions (dark lines are medians; dark shading covers the 50% intervals; light shading covers the 90% intervals) for historical (1950–2018) and projected age-1+ abundance (in absolute terms and relative to MNPL) and mortality due to all sources for the base-case operating model and management strategy "A". The grey vertical line indicates the start of the projection period (2018).



less than that for the base-case operating model. In contrast with the base-case operating model, not implementing management of bycatch (management strategy A) or assuming a high value for R_{MAX} (management strategy M) leads to much poorer performance for harbor porpoises than was the case for the base-case operating model. The results for grey seals are more promising for this operating model because there is an appreciable probability that $MSYR_{1+}$ is less than 0.06 under the base-case operating model (Fig. 2).

Changing MNPL/K from 0.6 to 0.5 has little effect on the fits to the data for harbor porpoises and grey seals, but the fit to the

Table 7. Values for the performance metrics for five of the seven operating models and five of the management strategies.

Operating model–management strategy	Probability of exceeding MNPL (%)						Cod effort			Lumpfish effort			Cod effort			Lumpfish effort		
	Years 15–20			Years 95–100			Years 15–20						Years 95–100					
	HP	HS	GS	HP	HS	GS	HP	HS	GS	HP	HS	GS	HP	HS	GS	HP	HS	GS
Base-case																		
Reference	99.8	68.0	91.8	100.0	100.0	100.0	0.27	0.05	0.12	0.26	0.05	0.12	0.25	0.04	0.15	0.24	0.04	0.16
A	95.9	0.0	32.6	99.0	0.0	54.5	1.00	0.99	1.00	0.99	0.99	0.99	1.00	1.01	0.99	1.00	0.99	0.99
D	99.0	0.0	33.0	100.0	0.4	56.6	0.12	0.00	0.00	0.99	0.99	0.99	0.06	0.00	0.00	1.00	0.99	0.99
E	99.0	0.0	33.0	100.0	0.4	57.5	0.00	0.00	0.00	0.99	0.99	0.99	0.00	0.00	0.00	0.99	0.99	0.99
L	99.9	83.7	92.7	100.0	100.0	100.0	0.18	0.11	0.10	0.18	0.11	0.10	0.10	0.08	0.07	0.09	0.08	0.07
M	98.8	68.0	91.8	99.1	100.0	100.0	0.62	0.05	0.12	0.60	0.05	0.12	0.58	0.04	0.15	0.57	0.04	0.16
$N_{1950}/K \sim$ U[0.5, 0.7]																		
Reference	99.9	63.0	90.8	100.0	100.0	100.0	0.28	0.05	0.12	0.28	0.05	0.12	0.26	0.04	0.15	0.26	0.04	0.17
A	84.6	0.0	25.8	91.7	0.0	61.6	1.00	0.99	1.00	0.99	0.99	0.99	1.00	1.01	0.99	0.99	0.99	0.99
D	98.3	0.0	26.3	100.0	0.0	63.9	0.13	0.00	0.00	0.99	0.99	0.99	0.09	0.00	0.00	0.99	0.99	0.99
E	99.9	0.0	26.3	100.0	0.0	63.8	0.00	0.00	0.00	0.99	0.99	0.99	0.00	0.00	0.00	1.00	0.99	1.00
L	100.0	81.2	91.6	100.0	100.0	100.0	0.19	0.11	0.10	0.19	0.11	0.11	0.11	0.07	0.08	0.10	0.07	0.08
M	94.8	63.0	90.8	98.6	100.0	100.0	0.64	0.05	0.12	0.65	0.05	0.12	0.62	0.04	0.15	0.61	0.04	0.17
$MSYR_{1+}$ is set to 0.02 for harbor porpoise and 0.06 for the seal species																		
Reference	32.1	0.0	100.0	99.9	96.1	100.0	0.28	0.04	0.14	0.28	0.04	0.14	0.26	0.02	0.18	0.26	0.02	0.18
A	6.5	0.0	54.0	19.6	0.0	88.1	1.00	0.99	1.00	0.99	0.99	0.99	1.00	1.01	1.00	1.00	0.99	0.99
D	30.7	0.0	55.3	99.5	0.0	88.7	0.13	0.00	0.00	0.99	0.99	0.99	0.09	0.00	0.00	1.00	0.99	0.99
E	40.8	0.0	55.3	99.7	0.0	88.9	0.00	0.00	0.00	0.99	0.99	0.99	0.00	0.00	0.00	0.99	0.99	0.99
L	40.8	0.0	100.0	100.0	99.9	100.0	0.19	0.08	0.11	0.19	0.08	0.11	0.11	0.04	0.09	0.10	0.04	0.08
M	4.9	0.0	100.0	40.9	96.1	100.0	0.64	0.04	0.14	0.64	0.04	0.14	0.62	0.02	0.18	0.62	0.02	0.18
MNPL/K = 0.5																		
Reference	98.5	4.2	91.2	100.0	100.0	100.0	0.28	0.04	0.12	0.28	0.05	0.12	0.27	0.03	0.16	0.26	0.03	0.16
A	85.9	0.0	29.4	88.6	0.0	53.4	1.00	0.99	1.00	0.99	0.99	0.99	1.00	1.01	1.00	0.99	0.99	0.99
D	97.4	0.0	30.5	100.0	0.0	55.1	0.13	0.00	0.00	0.99	0.99	0.99	0.09	0.00	0.00	0.99	0.99	0.99
E	98.0	0.0	30.4	100.0	0.0	55.0	0.00	0.00	0.00	0.99	0.99	0.99	0.00	0.00	0.00	1.00	0.99	0.99
L	98.7	13.2	91.9	100.0	100.0	100.0	0.19	0.10	0.10	0.19	0.10	0.10	0.10	0.05	0.07	0.10	0.06	0.07
M	93.0	4.2	91.2	97.1	100.0	100.0	0.65	0.04	0.12	0.65	0.05	0.12	0.63	0.03	0.16	0.61	0.03	0.16
Ignore the two kinship-based estimates of abundance for harbor porpoise																		
Reference	100.0	68.0	91.8	100.0	100.0	100.0	0.26	0.05	0.12	0.25	0.05	0.12	0.24	0.04	0.15	0.24	0.04	0.16
A	92.9	0.0	32.6	96.8	0.0	54.5	1.00	0.99	1.00	0.99	0.99	0.99	1.00	1.01	0.99	1.00	0.99	0.99
D	99.9	0.0	33.0	100.0	0.4	56.6	0.11	0.00	0.00	0.99	0.99	0.99	0.05	0.00	0.00	1.00	0.99	0.99
E	100.0	0.0	33.0	100.0	0.4	57.5	0.00	0.00	0.00	0.99	0.99	0.99	0.00	0.00	0.00	0.99	0.99	0.99
L	100.0	83.7	92.7	100.0	100.0	100.0	0.17	0.11	0.10	0.17	0.11	0.10	0.09	0.08	0.07	0.09	0.08	0.07
M	97.4	68.0	91.8	99.4	100.0	100.0	0.59	0.05	0.12	0.58	0.05	0.12	0.56	0.04	0.15	0.57	0.04	0.16
90% of the seal bycatch mortalities are juveniles of age-0																		
Reference	100.0	1.0	91.3	100.0	100.0	100.0	0.26	0.07	0.14	0.26	0.07	0.15	0.25	0.07	0.22	0.24	0.07	0.23
A	96.4	0.0	54.7	99.0	0.2	87.7	0.99	0.98	0.98	1.00	1.00	0.98	0.99	0.99	0.99	1.00	1.00	0.99
D	100.0	0.0	55.5	100.0	0.9	88.1	0.11	0.00	0.00	1.00	1.00	0.98	0.06	0.00	0.00	1.00	1.00	0.99
E	100.0	0.0	55.5	100.0	1.0	88.1	0.00	0.00	0.00	1.00	1.00	0.98	0.00	0.00	0.00	1.00	1.00	0.99
L	100.0	2.0	92.1	100.0	100.0	100.0	0.18	0.13	0.12	0.18	0.13	0.12	0.10	0.10	0.10	0.10	0.10	0.10
M	99.2	1.0	91.3	99.8	100.0	100.0	0.60	0.07	0.14	0.59	0.07	0.15	0.57	0.07	0.22	0.58	0.07	0.23

Note: HP, harbor porpoise; HS, harbor seal; GS, grey seal.

estimates of abundance for harbor seals is somewhat misspecified (Supplementary Fig. S4[2]). However, the qualitative behavior of the management strategies is similar to that for the base-case operating model. Assuming that 90% of the bycatch mortality of seals in the cod and lumpfish fisheries is of age-0 juveniles does not affect the quality of the fits to the data. However, the estimates of age-1+ abundance for grey seals are scaled down (Supplementary Fig. S6[2]). The recovery of harbor seals is initially slower for this operating model, but harbor and grey seals recover to well above MNPL after 95–100 years under the reference management strategy and management strategies L and M. The recovery probability for grey seals for management strategies D, E, and L is notably higher for this operating model than for the base-case operating model. The values for the performance metrics are not very sensitive to the CV of the bycatch rate (although outcomes are somewhat more variable with higher CV; results not shown), nor to ignoring the two relative abundance indices (Supplementary Table 3[2]).

Discussion

We have developed an MSE framework that can be used to evaluate management options for the sources of human-caused mortality that affect harbor porpoises, harbor seals, and grey seals around Iceland. The results suggest that while the harbor porpoise population is above MNPL, this is not the case for harbor and grey seals, and reduction in bycatch mortality for these species is needed if the populations are to recover. The use of PBR, along with appropriate monitoring, is shown to be one way to provide limits on human-caused mortality that would allow for recovery of these populations.

The MSE developed here is unique for marine mammal MSEs in that the management strategies evaluated affect multiple species and there are multiple sources of mortality. Moreover, the results highlight the importance of taking a multispecies perspective because the amount and type of mitigation required differs between or among species owing to differences in productivity and

current status relative to MNPL. Separating sources of human-caused incidental mortality (bycatch mortality) by fishery (cod versus lumpfish) and direct mortality (by hunting and other deliberate means), as well as accounting for differences in the age classes impacted, provides managers with the ability to use the results to make tactical decisions at an operational scale.

MSE is a tool that can be used by countries to evaluate alternative ways to monitor abundance and strategies for managing human-caused mortality and hence the likelihood that their management system will achieve the goals of the US MMPA or their own conservation goals for marine mammals. The framework, which involves a population model-based assessment to parameterize an operating model that is specific to a given case followed by projections that consider case-specific implementation details, could be applied in other contexts, including those where less information is available than is the case here. Examples of situations in which this MSE framework could be applied outside of Iceland include bycatch of harbor porpoises and fishery interactions with harbor seals in Europe and bycatch of fur seals in trawl fisheries off South Africa, Namibia, Chile, New Zealand, and Australia. Each of these applications would involve case-specific sources of uncertainty.

The operating model for the MSE carried out for Iceland is based on fitting to available data on abundance. The fits are generally good (albeit noisy for harbor porpoises) and provide the basis for setting the values for the model parameters and assigning distributions to quantify uncertainty. The conditioned operating model provides a basis for conducting forecasts.

The Seafood Import Rule applies only to countries and fisheries that expect to export products to the USA. In the context of this study, that is assumed to be the Icelandic cod gillnet and perhaps lumpfish fisheries. The cod fishery is the largest source of human-caused mortality of harbor porpoises in Iceland, but the porpoise population is assessed to be above MNPL currently and is predicted to continue to increase despite current levels of human-caused mortality. In contrast, the major source of mortality for the two seal species is bycatch in the lumpfish fishery. Harbor seals, in particular, are declining, and unless the impacts of the lumpfish fishery are reduced, this downward trend is predicted to continue (e.g., Fig. 6). Thus, while the Seafood Import Rule is meant to reduce bycatch-related impacts on marine mammal populations, its application cannot guarantee that depleted populations will recover. This differs from the application of the MMPA in the US, which pertains to all fisheries. In the case of harbor seals in Iceland, the only way to achieve recovery to MNPL is to lower the impacts not only of the cod gillnet fishery but also of fisheries that may be exempt from the Seafood Import Rule but have impacts on harbor seals. Situations where some sources of human-caused mortality are subject to the rule and other sources, including other fisheries, are exempt from the rule are likely common in countries around the world. The management systems for such other fisheries could be based on other considerations and objectives and would not necessarily involve a formula such as eq. 1. Within such systems, the values for the parameters might be selected differently given the different objectives. An MSE framework such as that outlined in this paper could be used to compare alternative management schemes. It should be noted, of course, that marine mammals are affected by anthropogenic and environmental factors besides human-caused mortality due to fisheries. This paper has focused on human-caused mortality due to fisheries, but the effects of those other factors would influence rates of change for the three modelled species. Furthermore, the operating model is based on the assumption of density-dependent regulation, while alternative perspectives exist regarding how populations are regulated, including by selection-delayed growth (e.g., Witting 1997, 2003).

In the framework presented here, simply scaling fishery effort is the only way used to achieve bycatch reduction in the two fisheries. That is, however, not the only way to reduce bycatch, and it is likely that a mixture of approaches based on further analyses of the bycatch data would be used to reduce bycatch. Such approaches would include spatial and (or) temporal area closures, gear modifications or gear switching, or pingers or other deterrent devices.

The MSE in this paper analyzes multiple sources of human-caused mortality within the same framework. Accounting for all sources of human-caused mortality could have been more meaningful for seal pups and older individuals, but the impact of hunting and other forms of direct removal at current rates was minor compared with that of bycatch. The application of the PBR approach in this paper involved comparing total human-caused mortality (pups and non-pups in the case of seals) with the calculated PBR. It is possible that a management approach that accounted for the sex structure and age structure of future human-caused mortality would have achieved better outcomes, although the improvement in performance likely would have been small.

One of the reasons for the "optimistic" results for harbor porpoises is that the value for the parameter that determines productivity ($MSYR_{1+}$) was estimated in the conditioning process. In the case of grey seals, the posterior for $MSYR_{1+}$ is centered on the default value of 0.06, but the posteriors for this parameter for harbor porpoises and harbor seals are more optimistic and lead to more optimistic results, in the sense of a lesser depletion level at present and a faster rate of recovery under the management strategies considered. Results based on the values chosen to correspond to the default values for R_{MAX} for these stocks ($MSYR_{1+}$ = 0.02 for the harbor porpoise and 0.06 for the seals) lead to less optimistic outputs but in general to poorer fits to the available data. It is possible that improved performance would have been achieved by using control rules tailored to each species, in particular higher values of R_{MAX} for the species for which productivity is higher than was assumed during the development of the PBR formula.

Typically, there are insufficient data to estimate whether a population is above its MNPL (referred to as an OSP assessment in the US) for marine mammal populations; this is a principal reason that PBR was devised as a management framework (because it does not require knowing a population's status relative to OSP; Taylor et al. 2000). OSP assessments are best informed when data show a population recovering from a highly depleted state with low levels (or quantified levels) of anthropogenic mortality, growing at its maximum potential rate for some time, and then slowing in its growth rate due to density dependence effects (e.g., competition for resources). Under these conditions, it is possible to estimate the environmental carrying capacity (and thus the population size relative to this) and whether the population is above the inflection point (MNPL) level (and thus in the OSP range). However, these data conditions are rarely met for marine mammal populations. For example, of the 34 stocks of large cetaceans recognized in the USA, a formal OSP assessment has been completed only on the Eastern North Pacific stock of gray whales (*Eschrichtius robustus*).

The results of this study depend on the estimates of abundance. The simulations assume that a new abundance estimate becomes available to monitor population trends (and update the PBR) every 4 years. This is a reasonable assumption for the two seal species considered in this study, but at present there is only one reliable estimate of absolute abundance for harbor porpoises in Iceland, and that estimate is over 10 years old. Enhanced (i.e., more frequent) monitoring would allow recovery goals to be achieved with less variability in PBR levels (Brandon et al. 2017). In addition, more abundance estimates would lead to greater precision in the estimates of the parameters of the operating model. The parameters of the operating model are estimated by treating the human-caused removals as known. Reporting bycatch in logbooks is mandatory in Iceland, but compliance is not perfect. In addition,

reporting of removals by seal hunting was not mandatory until 2020. Direct estimates of bycatch rates are only available since 2010 so, while the estimates in Supplementary Appendix 2[2] are the best available, they are subject to uncertainty. Future work could consider additional operating models that account for uncertainty in the historical catches.

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