Fisheries Research 243 (2021) 106060

Contents lists available at ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

Performance metrics for alternative management strategies for gray seal-commercial fishery interactions in the Northwest Atlantic

André E. Punt [a,*], John R. Brandon [b], Douglas P. DeMaster [c], Paula T. Moreno [d]

[a] School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA, USA
[b] Independent Consultant, Pacifica, CA, USA
[c] Marine Analytical Consultants, LLC, PO Box 211082, Auke Bay, AK, USA
[d] Ecomarine Integrated Analytics, LLC, Pascagoula, MS, USA

ARTICLE INFO

Handled by Steven X. Cadrin

Keywords:
Gray seals
Simulations
Potential biological removal
Abundance estimation
Bycatch
Marine mammal-fisheries management

ABSTRACT

The Potential Biological Removal (PBR) level serves as a threshold for management of marine mammal–fishery interactions under the US Marine Mammal Protection Act. The PBR protocol involves classifying fisheries based on the ratio of recent average bycatch mortality to PBR. A simulation-based framework is developed that quantifies the probability of incorrectly concluding that average bycatch mortality exceeds PBR (i.e., a false positive) or incorrectly concluding that average bycatch mortality is less than PBR (i.e., a false negative), with application to the US stock of gray seals in the northwest Atlantic, a stock for which human-caused mortality levels are approaching PBR. The application to this stock of northwest Atlantic gray seals is complicated by the transboundary nature of the population. Consequently, the analyses are based on a population model that includes the US stock and the component of the Canadian stock off southern Nova Scotia, fitted to available data using Bayesian methods. The total error (i.e., false positive or false negative) probability is found to be largely independent of the coefficient of variation (CV) for estimates of bycatch mortality, whereas this probability is an increasing function of the CV for estimates of abundance. For gray seals, a CV for the estimates of abundance of ~0.2 appears to balance the reduction in the total error probability versus the cost of surveys with greater sampling effort and more precise estimates of abundance.

1. Introduction

The Potential Biological Removal (PBR) level serves as a threshold for management of marine mammal–fishery incidental interactions that result in serious injury/mortality (herein 'bycatch' or 'mortality') under the US Marine Mammal Protection Act (MMPA). The PBR system involves 'classifying' commercial fisheries based on the ratio of recent average bycatch to the PBR. The commercial fisheries that impact stocks for which human-caused mortality is greater than PBR trigger additional fisheries monitoring and management measures, including the creation of Take Reduction Teams aimed at reducing bycatch in commercial fisheries. Such measures are put in place to allow depleted stocks to recover to their Maximum Net Productivity Level (MNPL) if they are below it and to allow healthy stocks to be maintained above their MNPL, as mandated by the MMPA. In Canada, both intentional (nuisance kills and direct harvest) and incidental mortality of gray seals occur and are managed using a similar approach (albeit with reference points that differ from the USA's PBR management) (Hammill and Stenson, 2007, 2013; DFO, 2017; Hammill et al., 2017).

For stocks that have human-caused mortality levels approaching PBR, such as the US gray seal *Halichoerus grypus* stock, where the annual average removal rate is estimated at 68.61 % of PBR (average annual mortality in the USA 953 seals, consisting mostly of bycatch) (Hayes et al., 2021), the ramifications of management conclusions with respect to this threshold become more acute. Errors in the assessment of mortality levels relative to PBR have implications in terms of meeting statutory biological conservation objectives, as well as potential operational burdens for commercial fisheries in terms of adopting mitigation measures (e.g., spatio-temporal restrictions in fishing effort or gear modifications).

Transboundary stocks pose a major challenge to management of marine mammals by the range member countries, especially when essential information regarding movement (e.g., migration rates, permanent vs transient fractions and demographics of migrants) are poorly

* Corresponding author.
E-mail address: aepunt@uw.edu (A.E. Punt).

https://doi.org/10.1016/j.fishres.2021.106060
Received 1 April 2021; Received in revised form 26 June 2021; Accepted 29 June 2021
Available online 16 July 2021

understood or even unknown. Marine mammals are typically highly-mobile and many stocks are recognized as transboundary because they occur in more than one country's Economic Exclusive Zone (EEZ), or in one or more country's EEZ and international waters. In the USA, where the PBR management system has been applied for twenty-six years, PBR for transboundary stocks is either determined from the fraction of the stock in US waters (non-migratory stocks) or the entire stock (migratory stocks) (Anon, 2016). The uncertainties associated with management of transboundary stocks potentially lead to non-trivial errors in assessing mortality levels relative to PBR, and the robustness of the PBR management system in this context has not been investigated quantitatively.

Three distinct populations of gray seal occur worldwide: the western Atlantic, eastern Atlantic and Baltic populations. Bycatch of gray seals in commercial fisheries is prevalent throughout their range largely as a result of this species' distribution, life cycle and behavioral traits (Johnston et al., 2015; NMFS, 2020). The western Atlantic population is considered a meta-population with twenty-six breeding colonies presently known: 18 in Canada and 8 in the USA, where half of the US colonies occur in southern Massachussets and the other half in northern Maine (den Heyer et al., 2021). Gray seal abundance in the western North Atlantic was markedly reduced by hunting and the introduction of bounty programs in the 19th and 20th centuries, and they were extirpated in the USA by the mid-20th century (Wood et al., 2020). Gray seal numbers have been recovering in the USA and Canada for over 50 years, increasing from less than 20,000 animals in the 1960s to over 350,000 animals in 2007 (Bowen et al., 2003; den Heyer et al., 2017; Hammill et al., 2017). The most recent estimate of the number of gray seals in the western North Atlantic is best derived as the sum of Canadian animals in 2016 (424,300; CV = 0.12; Hammill et al., 2017) and USA animals in 2016 (27,131; CV = 0.19; Hayes et al., 2019) or 451,431 animals (CV = 0.11). Estimates of pup production at all gray seal breeding rookeries in 2016 were recently reported by den Heyer et al. (2021).

Observed rates of annual recovery for various rookeries or sub-populations have been reported by several authors for this species, including 11 % per year by Harding and Harkonen (1999), 12.8 % per year by Bowen et al. (2003), and 26.3 % per year by Wood et al. (2020). However, it should be noted that Wood et al. (2020) concluded that the observed rate of increase[1] was influenced by immigration of gray seals from Canadian waters. Recent estimates of the annual rate of increase for the Sable Island population of gray seals are between 4–5 % (Hammill et al., 2017). This reduced rate of increase likely reflects density dependent effects on the population as it recovers and approaches the average annual carrying capacity for this area. In the most recent stock assessment of gray seals in US waters, human-caused mortality (68.61 % of PBR, Hayes et al., 2021) is 18 times higher than estimated in the first stock assessment (Blaylock et al., 1995) and is one of the higher values for a marine mammal stock in the northeast region of the USA that does not exceed PBR.

The aim of this paper is to explore the consequences of alternative monitoring schemes for bycatch and abundance estimation (i.e., the precision with which abundance and bycatch are estimated) as they relate to the regime for governing marine mammal–commercial fishery interactions in US waters. Specifically, this study focuses on the probability of incorrectly concluding that bycatch mortality exceeds PBR for the US stock of gray seals when this is not the case (false positive), and failing to conclude that bycatch mortality exceeds PBR when that is the case (false negative). The approach involves simulations like those conducted by Wade (1998), Brandon et al. (2017), and Punt et al. (2018).

Unlike the simulations of Wade (1998), however, which were based on a generic cetacean and a generic pinniped, and those of Punt et al. (2018) that were based only on cetacean species, the analyses in this paper use actual data for the western North Atlantic population of gray seals to condition the underlying population dynamics model, with uncertainty in parameter values estimated using Bayesian methods. Furthermore, previous simulation testing of PBR assumed population dynamics and human-caused mortality applied to a single closed population. As a transboundary population, with some level of mixing between the US and Canadian stocks (Nowak et al., 2020), North Atlantic gray seals present a management scenario that was not evaluated in the original simulation testing of PBR. Therefore, the population dynamics model developed here considers both the US stock of gray seals as well as the segment of the Canadian stock off southern Nova Scotia, and takes into account evidence for movement (taken to be permanent) between the stocks.

2. Materials and methods

2.1. Overview of the simulation process

Fig. 1 provides an overview of the entire simulation process. The true model of the population dynamics (the operating model) was a two-region age- and sex-aggregated population dynamics model. This model was fitted to data on trend and bycatch data for the US and Canada stocks using Bayesian methods, with the posterior distribution represented by 3000 draws using Hamilton Monte Carlo (HMC) sampling.

The performance of each alternative monitoring scheme (choices for how frequently abundance is estimated and with what precision, the precision of bycatch estimation, how long it takes for survey and observer data to be used to provide estimates of abundance and bycatch respectively) was evaluated by conducting simulations in which PBR, calculated from simulated survey data, was compared to the average bycatch mortality every five years for a 25-year period, starting in 2018. This involved projecting a population trajectory into the future for each draw of a Bayesian posterior distribution under a assumption that bycatch mortality is proportional to abundance, and that bycatch mortality rates during 1999–2017 are representative of future bycatch mortality rates (steps A, B in Fig. 1; sensitivity runs were explored for the latter assumption regarding future bycatch mortality rates). Estimates of abundance and bycatch were then simulated using the chosen monitoring scheme and associated CVs (step C). Given the generated data, values for PBR and the 5-year average estimated bycatch mortality were calculated, and whether or not the average estimated bycatch exceeded this PBR was recorded (step E). This result was compared to whether the true (i.e., operating model) PBR (PBR^{True} in Fig. 1) exceeded the true recent bycatch mortality (steps D and F in Fig. 1).

2.2. The operating model

The operating model was a two-region (USA and southern Nova Scotia, hereafter referred to as Canada) age- and sex-aggregated population dynamics model in which production was determined by the generalized logistic (i.e., Pella-Tomlinson) form. Following Wade (1998), the shape parameter θ was set to 1 so that MNPL occurred at one-half of carrying capacity (i.e., MNPL = 0.5K). The population model allowed for permanent exchange[2] ("dispersal") between the USA and Canadian stocks, i.e.:

$$\begin{aligned} N_y^{'US} &= N_{y-1}^{US} + r\,N_{y-1}^{US}\left(1 - \left(N_{y-1}^{US}\big/K^{US}\right)^{\theta}\right) - C_{y-1}^{US} \\ N_y^{US} &= N_{y-1}^{'US}\left(1 - \phi^{US-CA}\right) + \phi^{CA-US} N_{y-1}^{'CA} \end{aligned} \tag{1a}$$

[1] The observed rate of increase (i.e., $1/N^*dN/dt$ at some time) will (ignoring transient effects caused by stochasticity, dispersal and age-structure effects) always be less than the intrinsic rate of growth, r, which is the rate of increase for a closed population in the limit of zero population size.

[2] A model in which movement is non-permanent did not fit the available data adequately.

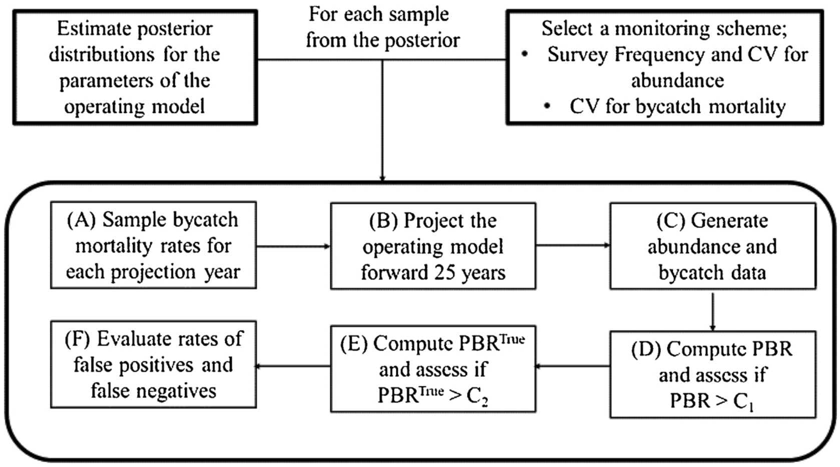

Fig. 1. Flowchart of the simulation process. PBR^{True} denotes the "true" (i.e., operating model) value for PBR (Eqn 5) and PBR denotes the value for PBR based on the simulated abundance data (Eqn 4). C_1 is the estimated average bycatch mortality for years *y*-A to *y*-A-4 and C_2 is the true bycatch mortality for years *y*-1 to *y*-5.

Table 1
Abundance-related data used for model fitting.

Quantity	Value
USA (2017)	27,131 (CV = 0.19) (Hayes et al., 2019)
Southern Nova Scotia (2016)	8966 (CV = 0.075)[a]
Rate of Increase (1988–2019; US)	0.1172 (SD 0.00141) (Supplementary Appendix B)

[a] : based on pup count information from den Heyer et al. (2017), and a ratio of total population/pup counts of 4.3 (DFO, 2017; NMFS, 2020) (Moreno et al., 2020).

$$\begin{aligned} N'^{CA}_y &= N^{CA}_{y-1} + r\,N^{CA}_{y-1}\left(1-\left(N^{CA}_{y-1}\big/K^{CA}\right)^{\theta}\right) - C^{CA}_{t-1} \\ N^{CA}_y &= N'^{CA}_{y-1}\left(1-\phi^{CA-US}\right) + \phi^{US-CA} N'^{US}_{y-1} \end{aligned} \quad (1b)$$

where N^a_y is the number of animals in region a (a=USA or Canada) at the start of year y, N'^a_y is the number of animals in region a after population growth and mortality but before dispersal, r is the intrinsic rate of growth (assumed to be the same for both regions); K^a is the nominal carrying capacity in region a; θ is a shape parameter (set to 1); ϕ^{a-b} is the dispersal rate from region a to region b (e.g., a = USA; b = Canada, or vice versa); C^a_y is the bycatch mortality in region a during year y, where $C^a_y = B^a_y N^a_y$; and B^a_y is the bycatch mortality rate for region a during year y.

The monitoring data generated using the operating model comprised periodic estimates of abundance and annual numbers of bycatch mortalities for the US fisheries, and where appropriate, Canadian fisheries. The estimates of abundance (based on pup counts extrapolated to the total population size; DFO, 2017) were assumed to be unbiased and log-normally distributed with respect to the true values, i.e.:

$$N^{obs,US}_y = N^{US}_y e^{\varepsilon_y - \sigma_I^2/2} \quad \varepsilon_y \sim N(0;\sigma_I^2) \quad (2)$$

where $N^{obs,US}_y$ is the generated abundance estimate for the US population for year y; and σ_I is the extent of observation error for the estimates of abundance. The estimates of bycatch mortality were also assumed to be unbiased and log-normal, i.e.:

$$C^{obs,US}_y = C^{US}_y\, e^{\eta_y - \sigma_C^2/2} \quad \eta_y \sim N(0;\sigma_C^2) \quad (3)$$

where $C^{obs,US}_y$ is the generated estimate of bycatch mortality for year y; and σ_C is the extent of observation error for the estimates of bycatch mortality.

Table 2
Time-series of bycatch mortality (see Supplementary Appendix A and Table 8.b of Moreno et al., 2020). Blank entries indicate missing values.

Year	USA	Canada
1999	155	
2000	193	
2001	117	
2002	0	
2003	242	
2004	573	
2005	574	
2006	248	
2007	902	
2008	634	
2009	1123	
2010	1453	
2011	1593	
2012	624	203.01
2013	1177	
2014	965	98.00
2015	1059	97.92
2016	531	93.03
2017	972	

2.3. Parameter estimation

The data available for parameter estimation were estimates of abundance (and their sampling CVs) for the USA and Canada (Table 1), estimates of bycatch mortality for the USA and Canada for 1999–2017 (Table 2; Supplementary Appendix A) and a rate of increase for the US population (Supplementary Appendix B; based on the trend in pup counts, under the assumption that trends in pup numbers reflect those in the total population). Bycatch estimates in Canadian waters were not directly available. Moreno et al. (2020) estimated bycatch in this region based on estimates of bycatch in US waters from two analogous fisheries and estimates of fishing effort reported to Northwest Atlantic Fisheries Organization. The CVs for the annual estimates of bycatch mortality

Table 3
The priors for the parameters of the population dynamics model. Note that the intrinsic rate of growth (r) is always pre-specified.

Quantity	Prior	Treatment in the base model
$\ln(N^a_{1985}/K)$	U[-112]	Estimated for the USA and Canada
$\ln K$	U[-∞, ∞]	Estimated for the USA; 20,000 for Canada
$\ln(1/B^a_y - 1)$	U[-∞,∞]	Estimated for Canada to USA; no dispersal from USA to Canada
$\ln(1/\phi^{Canada-US} - 1)$	U[-∞,∞]	Estimated for years with data (Table 2)

Table 4
Scenarios considered in the evaluation of the PBR approach, i.e. the base analysis and the sensitivity analyses. A dash indicates the same specification as the base analysis. The intrinsic rate of growth is 0.141 for all but sensitivity test J and dispersal from the USA to Canada is zero except for sensitivity tests B-E.

Case	A / B	Bycatch data used to fit the operating model	Abundance data used to fit the operating model	Future bycatch mortality rates	Dispersal / r / K / survey frequency
Base	2 / 2	Unbiased; CV = 0.2155	Unbiased; CV = 0.19	Samples from years with observer data	Only dispersal from Canada to the USA estimated; r = 0.141; survey takes place every 4 years
A	–	–	–	–	No dispersal
B	–	–	–	–	1% from USA to Canada
C	–	–	–	–	2% from USA to Canada
D	–	–	–	–	4% from USA to Canada
E	–	–	–	–	6% from USA to Canada
F	–	Unbiased; CV = 0.4	–	–	–
G	–	Unbiased; CV = 0.1	–	–	–
H	–	–	Unbiased; CV = 0.3	–	–
I	–	–	Positively biased by 50 %	–	–
J	–	–	–	–	r = 0.12
K	–	–	–	–	K (Canada) = 40,000
L	–	–	–	–	K (Canada) = 10,000
M	1 / 1	–	–	–	–
N	5 / 5	–	–	–	–
O	3 / 2	–	–	–	–
P	–	–	–	As for base, but allowing for a doubling in the expected rate from 2019 to 2046	–
Q	–	–	–	As for base, but allowing for a halving in the expected rate from 2019 to 2046	–
R	–	–	–	–	Survey takes place every 2 years

were assumed to be 0.2155 (the median of the CVs for 2008–2017; Supplementary Appendix A).

The (potentially) estimable parameters of the models were the intrinsic rate of growth, r; the ratio of the number of gray seals at the start of 1985 to K (i.e., N^a_{1985}/K^a); K by stock; the annual bycatch mortality rates; and the dispersal rates. However, several of the parameters were pre-specified for the 'base' model based on auxiliary information, with sensitivity tests used to explore the impact of different assumptions. Specifically the intrinsic rate of growth, the rate of dispersal from the USA to Canada, and the carrying capacity for the population off Canada were pre-specified. The value of the intrinsic rate of growth was determined by applying a population model to data for gray seals off Sable Island, Canada, leading to an estimate of 0.141 (Supplementary Appendix C). Annual bycatch mortality rates were estimated for the years with data (Table 2), with the remaining bycatch mortality rates set to the region-specific averages over the years with data. This implicitly assumes that the bycatch mortality rate (i.e., bycatch mortality as a fraction of population size) has been constant since 1985. The base model assumed that K for Canada is 20,000 and that there is no USA to Canada dispersal. The extent of Canada to USA dispersal was estimated (Table 3).

The likelihood function was based on the assumption that the estimates of abundance and bycatch mortality are log-normally distributed while the estimate for the observed rate of increase (the model estimate of which is the slope of log-abundance on time during 1988–2019; Supplementary Appendix B) was assumed to be normally distributed. Parameter estimation was achieved using Template Model Builder (Kristensen et al., 2016), with samples from the posterior obtained using the Hamiltonian Monte Carlo algorithm in the *tmbstan* function (Kristinsen, 2019) in R (R Core Team, 2020)[3] . For numerical stability reasons, priors were placed on the logarithms of N^a_{1985}/K^a and K, while the prior for B^a_y involved the transformation $\ell n(1/B^a_y - 1)$. The same transformation was used for the prior on the dispersal rates (Table 3). The HMC algorithm was run for three chains of 50,000 cycles each, with the first 25,000 cycles excluded as a warm-up. The chains were then thinned by retaining every 25th draw for a final set of 3000 parameter vectors.

2.4. *Projections and PBR application*

The population dynamics model was projected from 2018 to 2042, with the bycatch mortality rate for region a and future year y selected randomly from the values estimated for B^a_y for the years with observer data-based values (1999–2017 for the USA; 2012 and 2014−16 for Canada; Table 2), except for sensitivity tests P and Q (Table 4).

The PBR management approach for governing marine mammal-fishery interactions in US waters was applied to assess whether bycatch mortality exceeded that consistent with the goals of the MMPA (PBR). This involved comparing PBR in year y with the average of the estimates of bycatch mortality for years y-A-4 to y-A, where A is the time

[3] See Supplementary Appendix D for the TMB code for the model.

it takes for fishery observer data to be analysed to produce estimates of bycatch mortality (base-value, A = 2[4]). The PBR is the product of three parameters: (1) a minimum estimate of abundance that "provides reasonable assurance that the stock size is equal to or greater than the estimate"[5] (N_{MIN}); (2) one-half of the maximum intrinsic rate of population growth (0.50 R_{MAX}); and (3) a recovery factor (F_{R}) between 0.1 and 1.0 (Wade, 1998):

$$\mathrm{PBR} = N_{\mathrm{MIN}}\, 0.50\, R_{\mathrm{MAX}} F_{\mathrm{R}} \tag{4}$$

Calculations of PBR herein use: N_{MIN} = the lower 20th percentile of the log-normal distribution of the most recent abundance estimate (taken to be the value of $N_{y-\mathrm{B}}^{\mathrm{obs,US}}$ where B is the number of years that it takes to process raw survey data to produce an estimate of abundance; base value B = 2); default value for R_{MAX} for pinnipeds (0.12), as applied in the USA[6] ; and F_{R} = 1, appropriate for stocks at their "Optimum Sustainable Population" (OSP) level, which is between MNPL and K (Wade and Angliss, 1997; Wade, 1998). This follows the approach for calculating PBR in the most recent US gray seal stock assessment (Hayes et al., 2020). The lower 20th percentile of abundance estimates corresponding with N_{MIN} is currently used in practice, based on previous simulations where it met the policy goals of: 1) if the starting abundance level is ≥MNPL (e.g., ≥0.5K), abundance remains there or above (i.e., at OSP) for 20 years, and 2) if starting at 0.3K, the population recovers to at least MNPL within 100 years, with a 0.95 probability (Wade, 1998).

2.5. Evaluation and scenarios

The ratio of average bycatch mortality to PBR calculated for year y was compared to the true (i.e., operating model) value, which was defined as:

$$PBR_y^{\mathrm{True}} = 0.862 \text{ x } 0\ .50\, R_{MAX}\, N_y^{\mathrm{US}} \tag{5}$$

such that the key performance metric involves comparing whether I_1 and I_2 match or not, where

$$I_1 = \begin{cases} 1 & \frac{1}{5}\sum_{y'=y-5}^{y-1} C_y^{\mathrm{US}} > PBR_y^{\mathrm{True}} \\ 0 & \text{Otherwise} \end{cases} \tag{6a}$$

$$I_2 = \begin{cases} 1 & \frac{1}{5}\sum_{y'=y-\mathrm{A}-4}^{y-\mathrm{A}} C_y^{\mathrm{obs,US}} > PBR_{y-B} \\ 0 & \text{Otherwise} \end{cases} \tag{6b}$$

where C_y^{US} is the true (i.e. operating model) bycatch mortality for year y, and $C_y^{\mathrm{obs,US}}$ is the estimate of bycatch mortality for year y (lognormally distributed about C_y^{US}, Eqn 3). A false positive arises when $I_1 = 0$ and $I_2 = 1$ while a false negative arises when $I_1 = 1$ and $I_2 = 0$.

The value 0.862 in Eqn 5 accounts for the fact that the true abundance is taken from the operating model when PBR is based on the operating model. The choice of N_{MIN} = the lower 20th percentile of the log-normal distribution of the most recent abundance estimate in the standard PBR formula was selected so that policy goals of the MMPA related to population recovery are met, in particular when CV of the abundance estimates is 0.2 and the CV of bycatch mortality about PBR is 0.3 (Wade, 1998). For a population starting at 0.3 K, this leads to a distribution for population size relative to K after 100 years of PBR management that is centered around 0.570 (Fig. 2; Supplementary Fig. 1). The value 0.862 in Eqn 5 leads to projections based on seting PBR using Eqn 5 that would reach 0.570K after 100 years for a population initially at 0.3K (Supplementary Fig. 1).

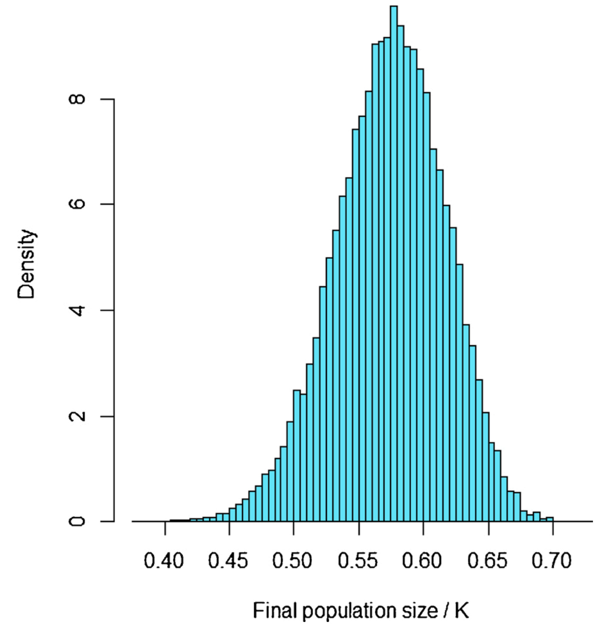

Fig. 2. Distribution for the population size after 100 years for a population initially at 0.3K when mortality is set to PBR and the CV of the estimates of abundance is 0.2. The numbers of animals dying due to serious injury and mortality are normally distributed about PBR with a CV of 0.3.

The base specifications for the parameters are: A = 2 and B = 2 (it takes two years for estimates of abundance and bycatch mortality to be processed); a CV for the abundance estimates of 0.19 (Table 1); and a CV for the estimate of annual bycatch mortality of 0.2155. The analyses also include alternative scenarios (Table 4) that explore sensitivity to these specifications, as well as to aspects of how the population assessment was undertaken, and to future trends in bycatch mortality rates.

3. Results

3.1. Fit of the two-region population model

Fig. 3 shows the best (i.e., maximum a posteriori [MAP] estimates) fits to the data for the two-region population dynamics model in terms of the fit to the abundance estimates and the estimates of bycatch mortality. The model also fits to the observed rate of increase for the USA based on the pup counts. In general, the MAP fits match the data very well (not unexpected given the low degrees of freedom). However, there are some exceptions. The model in which there is no dispersal from the Canadian stock to the US stock is unable to achieve the rate of recovery for the US stock, and infers that carrying capacity for the US stock is essentially infinite. This occurs because a higher estimate of carrying capacity leads to a higher inferred rate of increase (lesser density-dependent response), such that the rate of increase is then close to the observed rate of increase. Dispersal rates from the USA to Canada of 4% and 6% do not lead to adequate model fits. These three cases (A, D and E) are consequently not considered further.

The trace plots for the Bayesian analyses are not suggestive of a lack of convergence (see, for example, Supplementary Fig. 2), likewise Bayesian R-hat statistics were all near 1.0, which is consistent with convergence (Vehtari et al., 2021), and the posterior distributions for

[4] In the five most recent stock assessment reports for gray seals in US waters, estimates of bycatch in commercial fisheries were available within a two-year period (e.g., bycatch data from 2017 were included in the 2019 stock assessment).

[5] Sec. 3(27) Marine Mammal Protection Act

[6] The PBR was applied with R_{MAX} = 0.12 as that is the default value, but the operating model and underlying population dynamics (Eqns. 1a and 1b) were based on r = 0.141 for most scenarios.

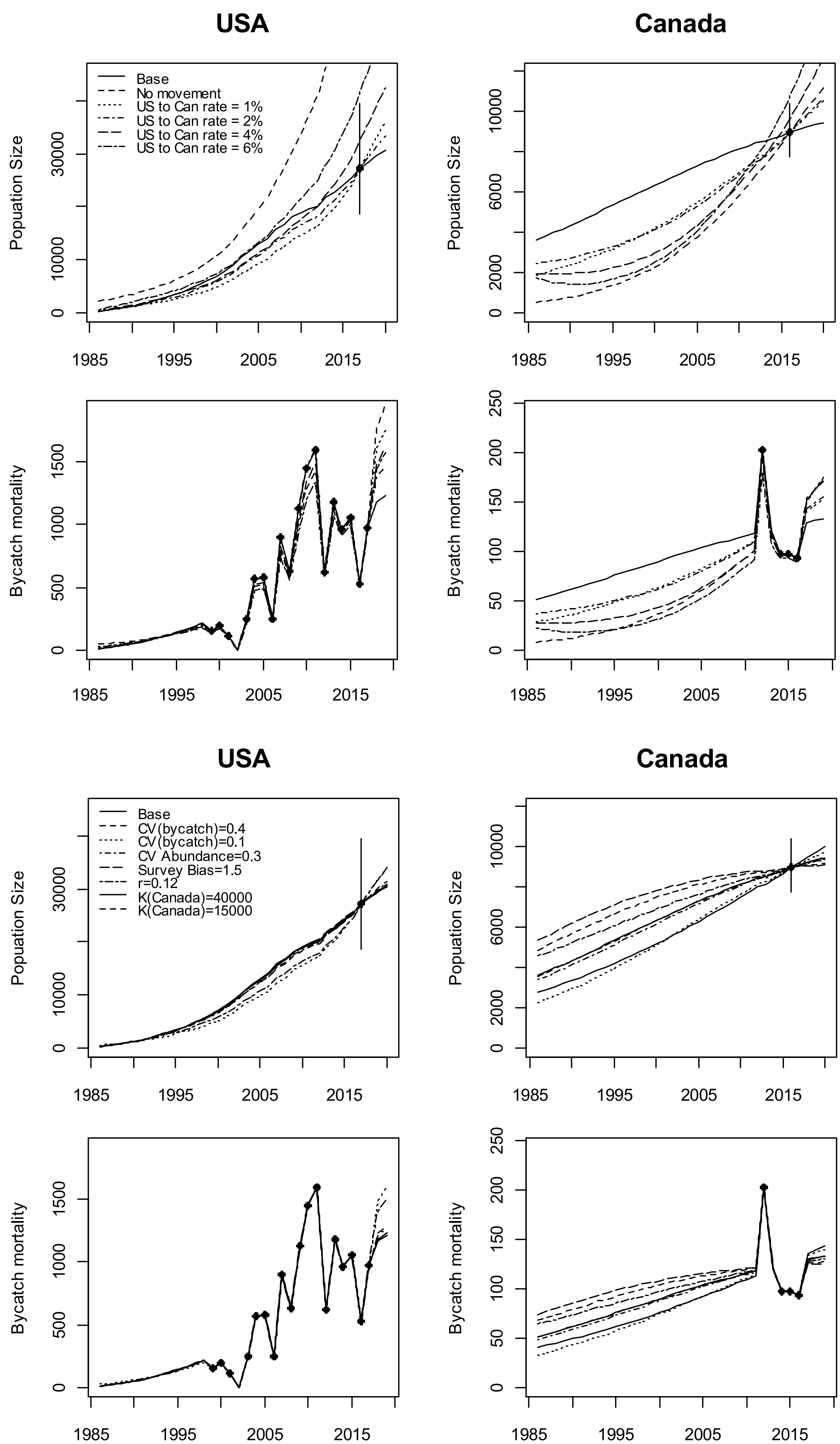

Fig. 3. Maximum a posteriori density ("best") estimates of the time-trajectories of total abundance and bycatch mortality (C_y^a). The 95 % CIs for the abundance estimates are denoted by the vertical lines in the population size plots. Note that K (Canada) is pre-specified. Results for different sets of sensitivity tests are provided in the upper and lower two sets of panels.

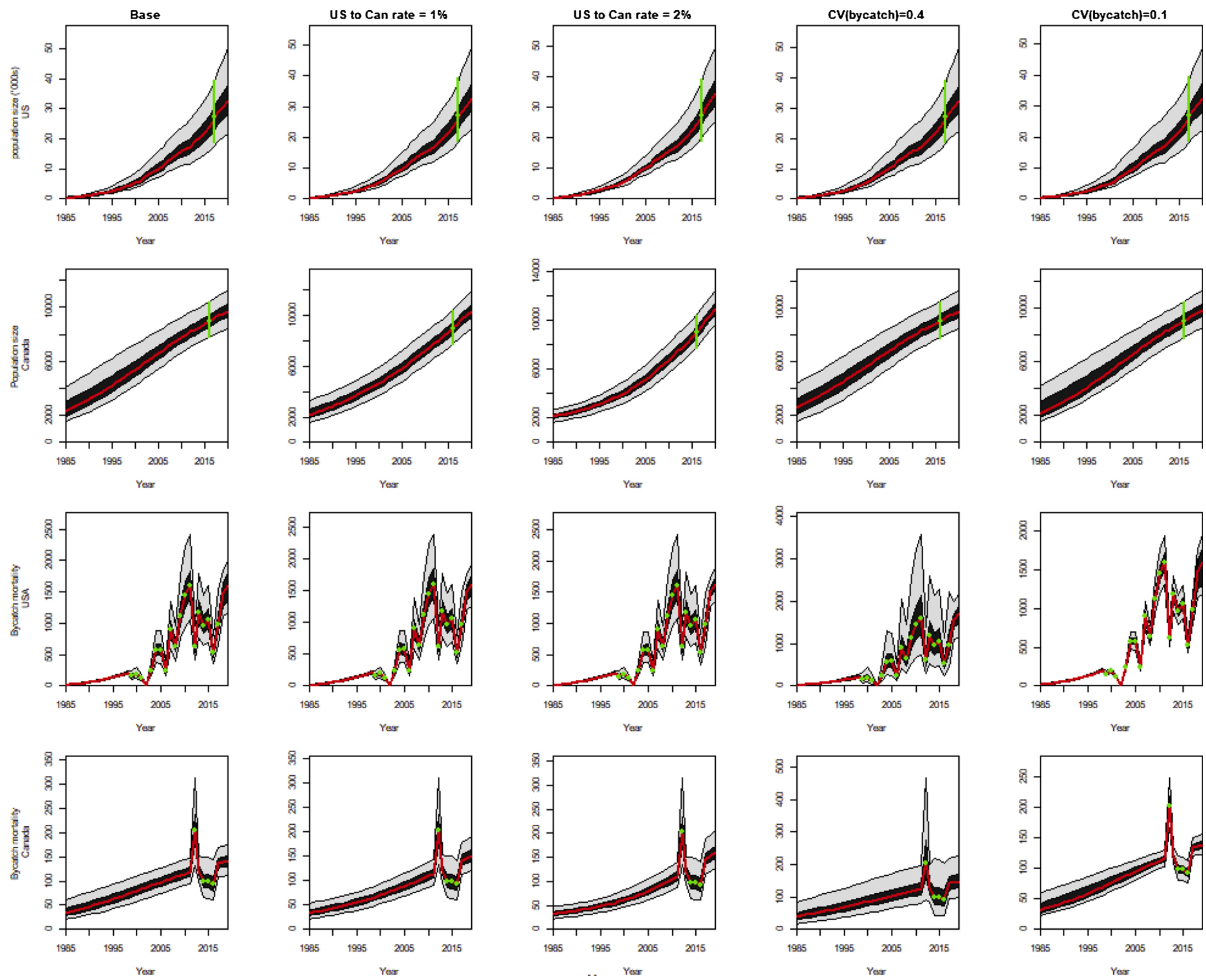

Fig. 4. Posterior distributions (red line medians, black areas 50 % CIs; grey shading 95 % CIs) for the time-trajectories of total abundance (adjusted as appropriate by survey bias), along with the estimates of abundance and their 95 % confidence intervals (green symbols and lines) (upper two rows of panels), and posterior distributions for annual human-caused bycatch mortality and the associated data points (lower two rows of panels).

the time-trajectories of abundance and bycatch mortality match the data well. Fig. 4 shows the posterior distributions for abundance and of human-caused mortality by stock (USA and Canada). The model adequately captures the trend in abundance for the US stock (the case with $r = 0.12$ leading as expected to among the poorer fits). There is more variation in the estimated historical time trajectory of abundance for the Canadian stock. This is because there is no reliable rate of increase information for the Canadian population in southwest Nova Scotia.

The posterior medians and 95 % intervals for the dispersal rate from Canada to the USA for the base model and cases B and C are: 0.040 (0.031, 0.050), 0.052 (0.044,0.065), and 0.069 (0.057, 0.085) respectively. These results support the premise that there is net movement from gray seal rookeries in Canada to rookeries in the USA and implies a negative correlation between the Canada to USA and USA to Canada dispersal rates given the constraint imposed by the observed rate of increase for the US stock.

3.2. Performance of monitoring schemes

Fig. 5 and Supplementary Fig. 3 illustrate the effects of the various monitoring schemes on the probability of a false positive (incorrectly concluding that bycatch mortality exceeds PBR when it does not) and the probability of a false negative (incorrectly concluding that bycatch mortality is less than PBR when it isn't). Fig. 5 and Supplementary Fig. 3 also show the total error probability (the probability of either a false positive or a false negative). The probabilities reported in Fig. 5 and Supplementary Fig. 3 integrate over time as well as over draws from the posterior distribution.

The probability of false positives and false negatives is largely independent of the CV of bycatch mortality (although there is a slight increasing trend in the probability of error and hence total error with increasing CV). In contrast, the CV of the abundance estimates has a marked impact on both the false positive and false negative (and hence total) probabilities. The probability of a false positive declines as the CV for the abundance estimates increases, while the probability of a false negative increases with increases to the CV of the abundance estimates. The total error probability is dominated by the probability of false positives because there are few true positives (the current bycatch mortality rate is ~3% for most of the cases, which is less than half of the true r - the exception is case P for which the rate of bycatch mortality increases with time).

3.3. Abundance estimation

The "optimal" CV for estimation of abundance is the lowest value considered, primarily because the probability of a false positive is minimized when the CV of the abundance estimates is low. This

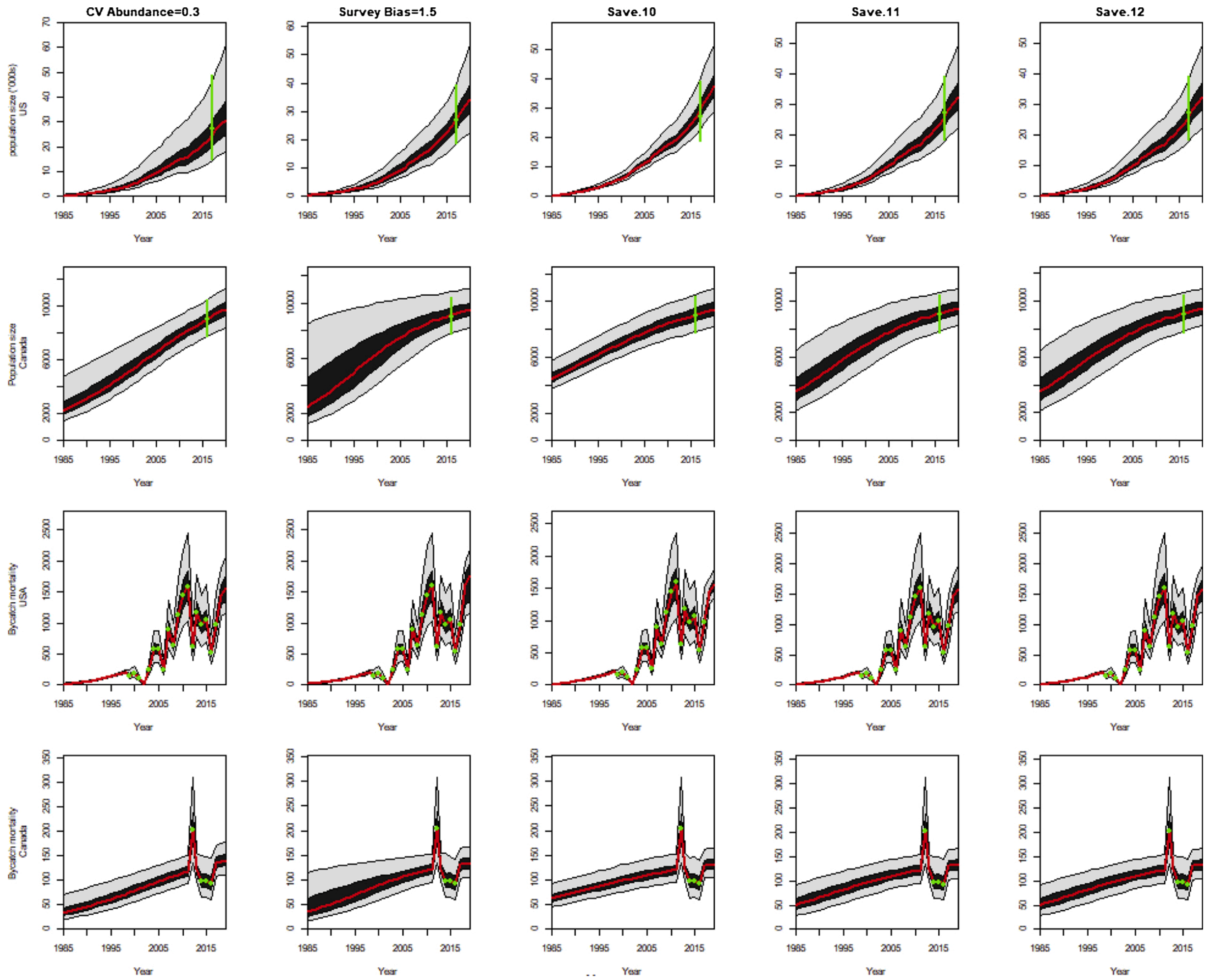

Fig. 4. (*continued*).

conclusion is robust to dispersal rate, true historical bycatch CV, the bias in estimates of abundance, the value of r, the value of K for the Canadian stock, the frequency of surveys, and the time needed to compute estimates of abundance and bycatch mortality. However, case P in which the bycatch mortality rate is increasing over time leads to more 'true positives' and hence an optimum CV for the abundance estimates of ~0.2 (even though the probability of false positive is lower for case P than for the remaining cases).

Compared to the base model, positively biased historical estimates of bycatch mortality (Case I), a lower value for r (case J), and the bycatch mortality rate halving over time (case Q) lead to noteworthy lower total error probabilities (reductions of 0.16, 0.09 and 0.12 respectively at the optimal CV compared to the base model). In contrast, a true (historical) CV for bycatch mortality of 0.4 (case F) and taking five years to produce estimates of abundance/bycatch mortality (case N) lead to a noteworthy higher total error probabilities (increases of 0.06, and 0.10 respectively at the optimal CV compared to the base model).

3.4. Estimation of bycatch

There is little difference in total error probability among choices for the CV of the estimates of bycatch mortality. However, the total error probability varies among cases, being highest for cases H (high true [historical] abundance CV) and N (taking five years to produce estimates of abundance/bycatch mortality) and lowest for cases I (a true [historical] CV for abundance of 0.4), J (a lower value for r), and Q (halving of the bycatch mortality rate over time).

4. Discussion

4.1. Population assessment

The analyses of this paper are based on a two-stock population dynamics model for gray seals in northwestern Atlantic fitted to data on abundance and bycatch mortality using Bayesian methods. There are few population-model based assessments for marine mammals and, very few of these allow for multiple stocks that mix and exchange individuals, apart from assessments of polar bears (e.g., USA-Canadian stocks) and those conducted by the Scientific Committee of the International Whaling Commission as the basis for management strategy evaluation for baleen whales subject to commercial and aboriginal harvest (Punt, 2017).

The population dynamics model allows for dispersal from the USA to Canada and vice versa. The model was only able to mimic the observed rate of increase for the US stock of 0.1172 (SD 0.00141) when some allowance was made for dispersal from Canada to the USA (base model posterior median 0.040), as ignoring dispersal completely led to poor fits to the data (Case A; Fig. 3). These results suggest an upper bound of ~2% of the US stock dispersing to Canada annually – rates greater than this lead to an inability to fit the abundance estimate for the USA (cases D and E in Fig. 3) and would correspond to very high Canada to the USA dispersal rates, given a 2% USA to Canada dispersal rate corresponds to a (posterior median) Canada to USA dispersal rate of almost 7%. Movement needs to be permanent to enable the model to mimic the data, given an observed rate of increase of almost 12 % for the USA stock

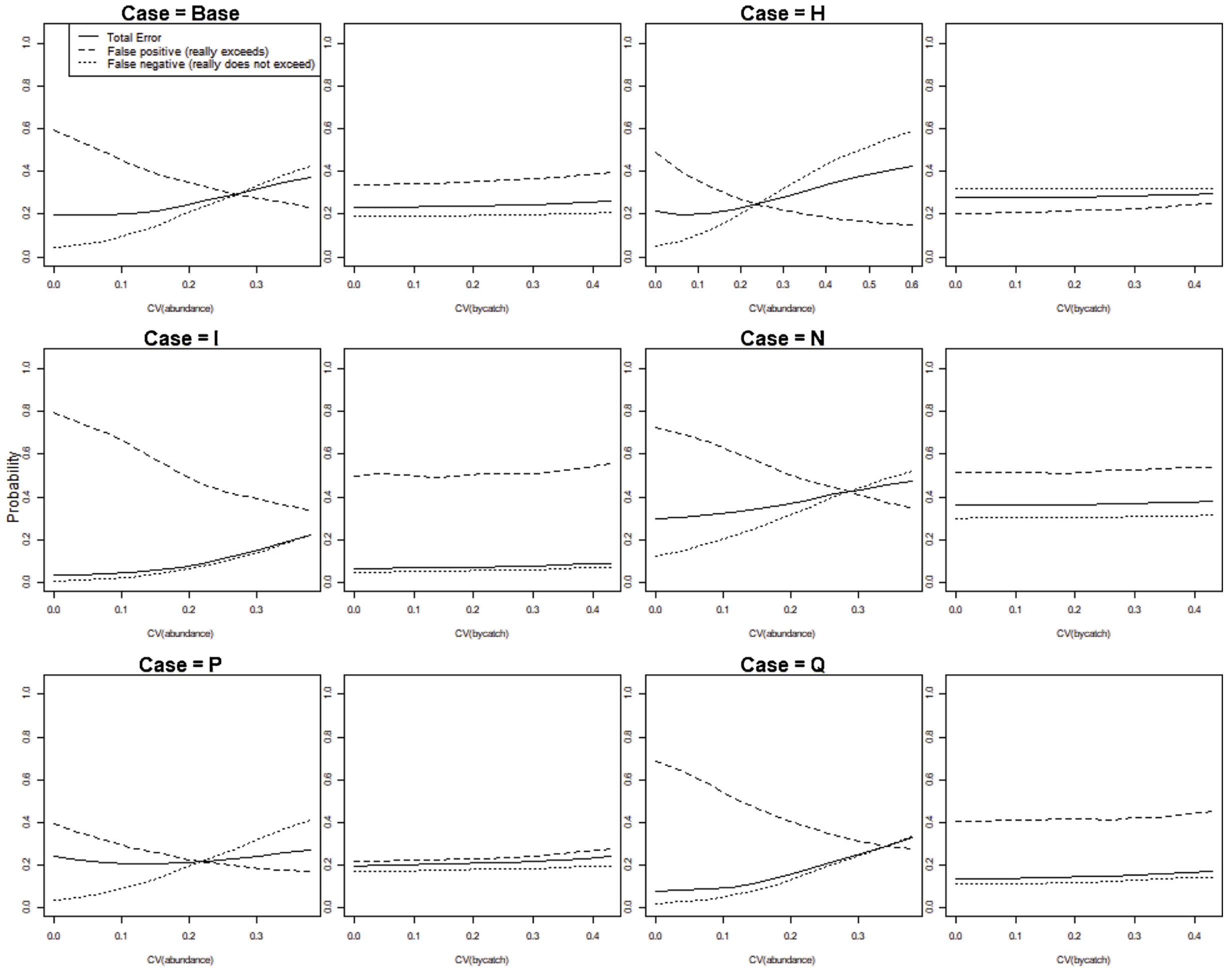

Fig. 5. Probability of false positives (dotted lines), false negatives (dashed lines) and total error (solid lines) as function of the CVs for abundance and bycatch for a subset of the cases in Table 4. The CV for bycatch is 0.2155 for the analyses based on varying the CV for abundance, and the CV for abundance is 0.19 for the analyses based on varying the CV for bycatch.

combined with a maximum rate of increase of 14 % and a rate of bycatch mortality of ~3%. Without a net influx into the US stock of ~2−5% the modelled rate of growth cannot mimic the observed rate of increase. Although the magnitude of immigration of seals from Canada to the USA is unknown, there is evidence supporting a net influx (Wood et al., 2020; den Heyer et al., 2021).

The model pre-specified the intrinsic rate of growth based on analysis on pup data for Sable Island, Canada (Supplementary Appendix C). The use of the results of the analysis of the pup count data to infer the intrinsic rate of increase for gray seals relies on the assumption that trends in pups mimic those of the total population for the US stock, i.e. density-dependent effects are either negligible or impact adult demographic parameters such as survival. Evidence for the British grey seal (Russel et al., 2019; Thomas et al., 2019) suggest that pup survival may be density-dependent. The modelling framework could be modified to account for age-structure effects to allow differences in trends in pop abundance from those in total abundance to be distinguished (e.g., using approaches such as those of Hammill et al., 2017). It would have been possible to estimate *r* along with the dispersal parameters given the available data. However, the precision of the estimate of *r* in Supplementary Appendix C is such that the data included in the likelihood function would have provided little information to update the prior for *r*.

The population assessment of this paper is relatively data-poor in that there is only one estimate of absolute abundance for each stock, no trend information for the Nova Scotia component of the Canadian stock and no direct information on movement. Collection and analysis of data on movements from tagging studies (e.g., Moxley et al., 2020; Nowak et al., 2020) would enable priors to be placed on the dispersal rates. Similarly, additional estimates of abundance would allow for refinement of the estimates of population size, including the possibility of estimating *K* for the Canadian stock. The estimates of bycatch rate are fairly precise (e.g., Supplementary Fig. 4), but precision for more data poor situations could be improved by treating the logits of the bycatch rates as being drawn from a hyper-distribution, the parameters of which could be estimated subject to an (uninformative) hyper-prior. Future bycatch rates could then be selected from the posterior for the parameters of the hyper-prior.

4.2. Choice of monitoring schemes

The results of this study highlight that the CV for the estimates of abundance is more influential than the CV for the estimates of bycatch mortality in terms of the probability of false positives and false negatives as shown in previous simulation studies of cetacean stocks (Punt et al., 2018). This can be attributed to the assumption that the estimates of abundance and bycatch mortality are unbiased. Consequently, errors when estimating bycatch mortality tend to cancel each other out in the 5-year average used to assess whether recent bycatch mortality exceeds PBR. In contrast, the CV of the estimates of abundance directly impacts the PBR (Eqn 4), such that lower values for the CV lead to higher values for PBR, all else being equal.

It might be unexpected that the false positive probability decreases as the CV for the estimate of abundance is increased. This is primarily a consequence of the fact that N_{MIN} depends on the CV of the estimate of abundance. Use of the 20th percentile when defining N_{MIN} relates directly to the CV of abundance estimate such that (in simulations) the use of the PBR formula leads to higher probabilities of recovery when the CV for abundance is greater than 0.2 (Wade, 1998). A higher CV (i.e., greater than 0.2) for the abundance estimates consequently leads to a greater level of precaution than is "warranted" given the policy objectives.

This study provides no strong guidance regarding the ideal CV for estimation of bycatch mortality given that the total error probability is largely independent of this CV (Fig. 5; Supplementary Fig. 3). However, higher values for this CV lead to greater differences between true and estimated average bycatch mortality and hence perceptions regarding risk. A high CV for the estimates of bycatch mortality would lead to the perception (in some years) that the bycatch mortality is substantially in excess of PBR and hence perhaps lead to substantial restrictions on fisheries. Thus, while the results of this study do not support any CV for bycatch estimation, lower values are preferred.

In contrast, the "optimal" CV for the abundance estimates is the lowest value feasible (Fig. 5; Supplementary Fig. 3). However, the cost of reducing the CV of the abundance estimates may substantially exceed the benefit in terms of the reduction in the total error probability. The optimal CV for the abundance estimates increases from essentially zero to 0.08 (case I; positively biased historical estimates of bycatch mortality) and to 0.25 (case P; the rate of bycatch mortality increases with time) if a total error probability within 0.05 of the optimal is considered acceptable. The scenarios with more frequent surveys (every 2 vs every 4 years) did not impact the error probabilities noticeably. The lack of sensitivity to survey frequency within the range explored is not unexpected from the results of Punt et al. (2018, 2020) who performed exhaustive testing (including scenarios with varying *K*, initial depletion and the intrinsic rate of growth) and found that - for a generic marine mammal and three cetacean species with markedly different life-histories - survey frequency was less influential in terms of achieving conservation objectives than survey CV, and survey bias.

The results of the analysis of monitoring schemes is focused on the total error probability (the sum of the probabilities of false positives and false negatives), essentially implying that the consequences of each type of error is equal. The selection of an 'optimal' CV could be based on weighting false positive and false negative probabilities differently, reflecting their relative consequences (to the fishery and to the population respectively). Given cost estimates for surveys, this framework could be used to inform optimal levels of survey effort (if the relationship between effort and the CV is assumed) in terms of achieving some acceptable target for error rates (false negative, false positive, or total).

The projections are based on a fairly simple (age- and sex-aggregated) population dynamics model and assume that monitoring will occur as simulated. Future work could consider basing projections on an age- and sex-structured population dynamics model to better account for time-lags (such models already exist for gray seal populations in Canada (Hammill et al., 2017; DFO, 2017) and the United Kingdom (Thomas et al., 2019)). The model of the population dynamics ignores the process error caused by inter-annual variation in expected birth and survival rates (i.e., environmental variation), factors known to impact the performance of PBR-based management (Punt et al., 2018, 2020; demographic stochastity will be largely inconsequential for gray seals in the northwest Atlantic, however, given their relatively large population sizes). While the assumption of annual estimates of bycatch mortality is reasonable, the assumption of survey estimates of total abundance every four (or two) years is not entirely consistent with recent practice that has focused on estimation of gray seal relative abundance through pup counts. Additional simulations are required to better understand any biases or uncertainties introduced by estimating abundance using pup counts and a multiplier based on life history data from a depleted population. Furthermore, the current CV for abundance for the US gray seal stock (and the resulting PBR value) is not calculated based on survey effort in the USA. The current US value (CV = 0.19) is "borrowed" from the CV of abundance that has been calculated for the Canadian population (Hayes et al., 2020).

4.3. Conclusions

Previous evaluations of the performance of the PBR system for managing mammal–fishery interactions (e.g., Wade, 1998; Brandon et al., 2017; Punt et al., 2018, 2020) have focused on the ability to achieve conservation objectives and to a lesser extent the probability of correctly assessing whether fisheries are correctly classified or did so without accounting for transboundary effects on managed stocks (Punt et al., 2018). This study explores the impact of monitoring on the probability of incorrectly concluding bycatch mortality is less than PBR when it is not and incorrectly concluding bycatch mortality is greater than PBR when it is not, with an application to gray seals on the northwest Atlantic. The application is unique in that it is based on an operating model that is fitted to the available data and accounts for the transboundary nature of managing bycatch of northwest Atlantic gray seals. Previous analyses suggest that application of PBR management will achieve conservation goals in this region (in fact, the higher value for *r* used in this analysis implies that use of the PBR formula with the default $R_{MAX} = 0.12$ will achieve these goals faster, albeit at a higher probability of concluding that bycatch mortality exceeds PBR when this is not the case). The results of this paper suggest that monitoring schemes can be selected to achieve both conservation and fishery goals, with a CV for the estimates of abundance for gray seals of ~0.2 likely to trade-off cost of surveys and likelihood of false positive and false negative errors.

CRediT authorship contribution statement

André E. Punt: Conceptualization, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Project administration. **John R. Brandon:** Conceptualization, Writing - review & editing. **Douglas P. DeMaster:** Conceptualization, Writing - review & editing. **Paula T. Moreno:** Conceptualization, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Matthieu Authier (CNRS-La Rochelle Université) for very helpful comments on an earlier version of this manuscript. Mike Hammill, Cornelia den Heyer and Garry Stenson (DFO), Kimberly Murray (NOAA, NEFSC) and Greg DiDomenico (Garden State Seafood Association) are thanked for providing information on the gray seals, bycatch and the associated fisheries. This research was conducted as part of the Independent Advisory Team for Marine Mammal Assessment, an effort funded by the Science Center for Marine Fisheries, a US National Science Foundation's Industry/University Cooperative Research Center.

References

Anon, 2016. Guidelines for Preparing Stock Assessment Reports Pursuant to the 1994 Ammendments to the MMPA. https://media.fisheries.noaa.gov/dam-migration/guidelines_for_preparing_stock_assessment_reports_2016_revision_gamms_iii_opr2.pdf.

Blaylock, R.A., Hain, J.W., Hansen, L.J., Palka, D.L., Waring, G.T., 1995. Gray Seal (*Halichoerus grypus*): Western North Atlantic Stock. US Atlantic and Gulf of Mexico

marine Mammal Stock Assessment Report. NOAA Technical Memorandum NMFS-SEFSC-363, pp. 117–119. https://repository.library.noaa.gov/view/noaa/9168.
Bowen, W.D., McMillan, J.I., Mohn, R., 2003. Sustained exponential population growth of grey seals at Sable Island. ICES J. Mar. Sci. 60, 1265–1374.
Brandon, J.R., Punt, A.E., Moreno, P., Reeves, R.R., 2017. Towards a tier system approach for calculating limits on human-caused mortality of marine mammals. ICES J. Mar. Sci. 74, 877–887.
den Heyer, C.E., Lang, S.L.C., Bowen, W.D., Hammill, M.O., 2017. Pup production at Scotian Shelf grey seal (*Halichoerus grypus*) colonies in 2016. DFO Can. Sci. Advis. Sec. Res. Doc. 34, 2017/056. v +. https://waves-vagues.dfo-mpo.gc.ca/Library/40617725.pdf.
den Heyer, C.E., Bowen, W.D., Dale, J., Gosselin, J.F., Hammill, M.O., Johnston, D.W., Lang, S.L.C., Murray, K.T., Stenson, G.B., Wood, S.A., 2021. Contrasting trends in gray seal (*Halichoerus grypus)* pup production throught the increasing northwest Atlantic metapopulation. Mar. Mamm. Sci. 37, 611–630.
DFO, 2017. Stock assessment of Canadian northwest Atlantic grey seals (*Halichoerus grypus*). DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 14, 2017/045, Quebec, Canada. https://waves-vagues.dfo-mpo.gc.ca/Library/40646749.pdf.
Hammill, M.O., Stenson, G.B., 2007. Application of the precautionary approach and conservation reference points to the management of Atlantic seals. ICES J. Mar. Sci. 64, 702–706.
Hammill, M.O., Stenson, G.B., 2013. A discussion of the precautionary approach and its application to Atlantic seals. DFO Can. Sci. Advis. Sec. Res. Doc. 25, 2013/030. v+. https://waves-vagues.dfo-mpo.gc.ca/Library/349398.pdf.
Hammill, M.O., den Heyer, C.E., Bowen, W.D., Lang, S.L.C., 2017. Grey seal population trends in Canadian waters, 1960-2016 and harvest advice. DFO Can. Sci. Advis. Sec. Res. Doc. 30, 2017/052. v +. https://waves-vagues.dfo-mpo.gc.ca/Library/40643542.pdf.
Harding, K.C., Harkonen, T.J., 1999. Development in the Baltic grey seal (*Halichoerus grypus*) and ringed seal (*Phoca hispida*) populations during the 20th century. Ambio 28, 619–627.
Hayes, S.A., Josephson, E., Maze-Foley, K., Rosel, P.E., 2019. US Atlantic and Gulf of Mexico marine mammal stock assessments – 2018. US Dept Commer, Northeast Fish Sci Cent. NOAA Technical Memorandum NMFS-NE-258, Woods Hole, MA, p. 298. https://repository.library.noaa.gov/view/noaa/20611.
Hayes, S.A., Josephson, E., Maze-Foley, K., Rosel, P.E., 2020. US Atlantic and Gulf of Mexico marine mammal stock assessments – 2019. US Dept Commer, Northeast Fish Sci Cent. NOAA Technical Memorandum NMFS-NE-264, Woods Hole, MA, p. 472. https://media.fisheries.noaa.gov/dam-migration/2019_sars_atlantic_508.pdf.
Hayes et al., in press. US Atlantic and Gulf of Mexico Marine Mammal Stock Assessments – 2020. US Dept Commer, Northeast Fish Sci Cent, NOAA Technical Memorandum NMFS-NE-258, Woods Hole, MA.
Johnston, D.W., Frungillo, J., Smith, A., Moore, K., Sharp, B., Schuh, J., Read, A.J., 2015. Trends in stranding and by-catch rates of gray and harbor seals along the northeastern coast of the United States: evidence of divergence in the abundance of two sympatric phocid species? PLoS One 10, e0131660.
Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., Bell, B.M., 2016. TMB: automatic differentiation and Laplace approximation. J. Statist. Soft. 70, 1–21.
Kristinsen, K., 2019. Package 'tmbstan'. https://cran.r-project.org/web/packages/tmbstan/tmbstan.pdf.
Moreno, P.T., DeMaster, D.P., Punt, A.E., Brandon, J.R., 2020. Estimates of Human-caused Removals of Gray Seals in the Northeast U.S. Atlantic and Adjacent Canadian Waters: Preliminary Implications for PBR-based Management. Report to Science Center for Marine Fisheries (SCEMFIS), p. 36. https://scemfis.org/wp-content/uploads/2020/10/Report_Gseal_removals_IAT.pdf.
Moxley, J.H., Skomal, G., Chisholm, J., Halpin, P., Johnston, D.W., 2020. Daily and seasonal movements of Cape Cod gray seals vary with predation risk. Mar, Eco. Progr. Ser. 644, 215–228.
NMFS, 2020. Gray seal (halichoerus grypus grypus): Western North Atlantic stock. In: Hayes, S.A., Josephson, E., Maze-Foley, K., Rosel, P.E. (Eds.), Draft US Atlantic and Gulf of Mexico Marine Mammal Stock Assessments, pp. 96–103, 2012. https://media.fisheries.noaa.gov/dam-migration/2019_sars_atlantic_508.pdf.
Nowak, B.V.R., Bowen, W.D., Whoriskey, K., Lidgard, D.C., Mills Flemming, J.E., Iverson, S.J., 2020. Foraging behaviour of a continental shelf marine predator, the grey seal (*Halichoerus grypus*), is associated with in situ, subsurface oceanographic conditions. Move. Ecol. 8, 41.
Punt, A.E., 2017. Review of contemporary cetacean stock assessment methods. J. Cetacean Res. Manage. 17, 35–56.
Punt, A.E., Moreno, P., Brandon, J.R., Matthews, M.A., 2018. Conserving and recovering vulnerable marine species: a comprehensive evaluation of the US approach for marine mammals. ICES J. Mar. Sci. 75, 1813–1831.
Punt, A.E., Siple, M., Francis, T.B., Hammond, P.S., Heinemann, D., Long, K.J., Moore, J. E., Sepúlveda, M., Reeves, R.R., Sigurðsson, G.M., Víkingsson, G., Wade, P.R., Williams, R., Zerbini, A.N., 2020. Robustness of Potential Biological Removal (PBR) to monitoring, environmental and management uncertainties. ICES J. Mar. Sci. 7-8, 2491–2507.
R Core Team, 2020. R: a Language and Environment for Statistical Computing. URL. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Russel, D.J.F., Morris, C.D., Duck, C.D., Thompson, D., Hiby, L., 2019. Monitoring long-term changes in UK grey seal pup production. Aquat. Consev: Mar. Freshw. Ecosyst. 29 (S1), 24–39.
Thomas, L., Russell, D.J.F., Duck, C.D., Morris, C.D., Lonergan, M., Empacher, F., Thompson, D., Harwood, J., 2019. Modelling the population size and dynamics of the British grey seal. Aquat. Conserv: Mar. Freshw. Ecosyst. 29 (S1), 6–23.
Vehtari, A., Gelman, A., Simpson, D., Carpenter, B. and Bürkner, P-C., In press. Rank-normalization, folding, and localization: An improved $\widehat{R}$ for assessing convergence of MCMC. Bayes. Anal. https://arxiv.org/pdf/1903.08008.pdf.
Wade, P.R., 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. Mar. Mamm. Sci. 14, 1–37.
Wade, P.R., Angliss, R.P., 1997. Guidelines for Assessing Marine Mammal Stocks: Report of the GAMMS Workshop, April 3-5, 1996. NOAA Technical Memorandum NMFS-OPR-12. https://repository.library.noaa.gov/view/noaa/15963.
Wood, S.A., Murray, K.T., Josephson, E., Gilbert, J., 2020. Rates of increase in gray seal (*Halichoerus grypus atlantica*) pupping at recolonized sites in the United States, 1988-2019. J. Mamm. 101, 121–128.