















## Original Article

# Robustness of potential biological removal to monitoring, environmental, and management uncertainties

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The potential biological removal (PBR) formula used to determine a reference point for human-caused mortality of marine mammals in the United States has been shown to be robust to several sources of uncertainty. This study investigates the consequences of the quality of monitoring on PBR performance. It also explores stochastic and demographic uncertainty, catastrophic events, sublethal effects of interactions with fishing gear, and the situation of a marine mammal population subject to bycatch in two fisheries, only one of which is managed. Results are presented for two pinniped and two cetacean life histories. Bias in abundance estimates and whether there is a linear relationship between abundance estimates and true abundance most influence conservation performance. Catastrophic events and trends in natural mortality have larger effects than environmental stochasticity. Managing only one of two fisheries with significant bycatch leads, as expected, to a lower probability of achieving conservation management goals, and better outcomes would be achieved if bycatch in all fisheries were managed. The results are qualitatively the same for the four life histories, but estimates of the probability of population recovery differ.

**Keywords:** bycatch, conservation, marine mammal, MSE, potential biological removal, simulation, uncertainty.

## Introduction

Managing anthropogenic impacts on marine mammal populations often involves identifying the causes, computing levels of impact that the populations can sustain, and implementing regulations designed to achieve the management goals. The key sources of human-caused mortality for many marine mammal populations are bycatch—entanglement, entrapment, and hooking by commercial fishing gear—or entanglement in aquaculture nets and ropes (Kemper *et al.*, 2003; Read, 2005; Reeves *et al.*, 2013). Although there are other sources of human-caused mortality of marine mammals, there is a general consensus among scientists and conservationists that bycatch mortality is the currently dominant driver of human-caused population declines worldwide, and the primary barrier to the recovery of many depleted populations (Gales *et al.*, 2003; Kovacs *et al.*, 2012; Reeves *et al.*, 2013; Lewison *et al.*, 2014; Avila *et al.*, 2018). Sublethal effects (e.g. a decrease in reproductive output) caused by interactions with fishing gear are less well studied and seldom the focus of management decisions (but see van der Hoop *et al.*, 2016a,b).

The 1994 amendments to the 1972 US Marine Mammal Protection Act (MMPA) created the potential biological removal (PBR) approach to determine the level of human-caused mortality marine mammal populations could be sustain while still allowing those populations to recover (Wade, 1998). The PBR approach is well suited to data-poor situations because the PBR formula requires only a recent estimate of abundance. The PBR formula (or variants thereof) has been applied to compute recommended limits on human-caused mortality for marine mammal populations in many parts of the world (e.g. in the Baltic Sea: Berggren *et al.*, 2002; in New Zealand: Slooten *et al.*, 2006; in Canada: Stenson *et al.*, 2012) and has been applied to other animals subject to human-caused mortality (e.g. birds and bats: Diffendorfer *et al.*, 2015).

The PBR formula 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” ( $N_{\text{MIN}}$ ); (ii) one-half of the maximum intrinsic rate of population growth ( $0.50 R_{\text{MAX}}$ ); and (iii) a recovery factor ( $F_{\text{R}}$ ) between 0.1 and 1.0 (Wade, 1998), i.e.

$$\text{PBR} = N_{\text{MIN}} 0.50 R_{\text{MAX}} F_{\text{R}} . \quad (1)$$

Within the United States, the default values of the PBR parameters used in most management applications are:  $R_{\text{MAX}} = 0.04$  for cetaceans and 0.12 for pinnipeds;  $N_{\text{MIN}}$  = the lower 20th percentile of the (lognormal) distribution for the most recent estimate of abundance; and  $F_{\text{R}}$  is selected depending on the conservation status of the stock (lower values for poorer conservation status; Barlow *et al.*, 1995; Wade and Angliss, 1997; Wade, 1998; Anon, 2016).

The values for the parameters of (1) were determined by Wade (1998) using simulations of a generic cetacean and a generic pinniped. Specifically, the value of the percentile of the distribution used to compute  $N_{\text{MIN}}$  was selected to achieve (i) a 0.95 probability of rebuilding a stock to its maximum net productivity level [MNPL, typically 50% of the stock’s carrying capacity (K)] within 100 years (the “recovery goal”), under ideal conditions when a stock is initially at 0.3 K, and (ii) a 0.95 probability that a stock starting at MNPL will still be at or above MNPL in 20 years. Values for  $F_{\text{R}} < 1$  were set to ensure that the recovery goal is met for highly depleted stocks or when some of the “ideal”

assumptions of the simulations used to specify the percentile on which  $N_{\text{MIN}}$  is based are violated.

Use of simulation to evaluate the performance of management systems is referred to as management strategy evaluation (MSE; Bunnefeld *et al.*, 2011; Punt *et al.*, 2016). MSE involves developing models of the entire management system (monitoring, decision making, and implementation) and projecting the simulated population forward to determine how well management objectives might be achieved. MSE has been used to understand the behaviour of the PBR approach (Wade, 1998; Brandon *et al.*, 2017; Punt *et al.*, 2018), and more generally to understand the behaviour of conservation and management systems, including those for marine mammal populations subject to hunting and bycatch (e.g. IWC, 2014, 2016, 2017a, b; Punt and Donovan, 2007; Punt *et al.*, 2016).

The MSE analyses conducted by Wade (1998) varied the value of  $R_{\text{MAX}}$  (0.04 or 0.12) and the precision of the abundance estimate,  $N_{\text{MIN}}$  [coefficient of variation (C.V.) = 0.2 or 0.8]. Wade (1998) also considered eight uncertainties related to potential biases in the estimates of  $R_{\text{MAX}}$ , abundance, and mortality, the interval between abundance surveys (4 or 8 years), and the value of MNPL (0.45 or 0.70 K). The values of the parameters of (1) used to apply the PBR approach in the United States are designed to be robust to these uncertainties. Recent simulation studies have explored the robustness of the PBR approach to other sources of uncertainty. For example, Punt *et al.* (2018) examined the consequences of demographic uncertainty and of transient age-structure effects. The latter, in particular, were found to influence the recovery probability of depleted populations, but it was also shown that reducing  $F_{\text{R}}$  from its default values could make the PBR robust to these sources of uncertainty.

The ability of the PBR approach to achieve its goals depends on the nature of how abundance is monitored. However, obtaining frequent, precise, and unbiased estimates of abundance for many marine mammals remains challenging. Consequently, this article explores various combinations of factors influencing the quality and quantity of the data on which PBR could be based.

Several sources of process uncertainty that have become evident in recent years could affect the performance of the PBR approach in achieving management objectives but have not yet been explored analytically. Specifically, although Punt *et al.* (2018) considered the effects of demographic uncertainty (individual variation in birth and death rates), they did not consider the effects of environmental stochasticity (probabilities of birth and death rates that are correlated among individuals) or catastrophic events, which are likely more consequential for management and have been observed in marine mammal populations (e.g. Vidal and Gallo-Reynoso, 1996; Preen, 2004; Van Bresseem *et al.*, 2014; Lane *et al.*, 2015). Other factors that could affect the performance of the PBR approach include the sublethal effects of entanglements in fishing gear (e.g. van der Hoop *et al.* 2016a, b), and the mainly sublethal (e.g. reduced feeding or reproductive rates) but sometimes lethal effects of noise from human activities (e.g. Cox *et al.*, 2006; Danil and St. Leger, 2011). The purpose of this study is to develop and apply a modelling framework to examine the effects of these uncertainties.

Another uncertainty considered in this study relates to the situation in which some, but not all, of the fisheries that impact a marine mammal population are managed. The Fish and Fish Product Import Provisions of the MMPA [Section 101(a)(2), implemented in 2016 81 FR 54389; hereafter referred to as the

“Seafood Import Rule”] require that a harvesting nation’s regulatory programmes address intentional and incidental (bycatch) mortality and serious injury to marine mammals in fisheries that export fish to the United States. The regulations require nations with fisheries that incur, or may incur, marine mammal bycatch (Export Fisheries), to adhere to marine mammal bycatch monitoring and mitigation standards “comparable” to those applied to US fisheries. To continue to import seafood to the United States, any nation with one or more Export Fisheries is required to “demonstrate that it had adopted and implemented . . . a regulatory program . . . that is comparable in effectiveness to the US regulatory program.” By 2021, the United States intends to make comparability findings to determine whether each nation’s marine mammal bycatch programme is “comparable” to that of the United States. If a foreign fishery fails the comparability finding, the fish or fish products from that fishery will be prohibited from entering the United States until the country applies again and the fishery is accorded a positive comparability finding. It is common for a marine mammal population to be subject to bycatch in multiple fisheries, and it is possible that in some countries not all of the fisheries with bycatch of marine mammals would be considered Export Fisheries if they do not export fish or fish products to the United States and hence subject to the MMPA requirements.

We therefore test the robustness of the PBR approach to previously unrecognized or unconsidered types of uncertainty, catastrophic changes, and spatial differences in implementation. Specifically, we asked: (i) what are the implications of uncertainties in monitoring (experiment # 1), (ii) is the PBR approach robust to cases where birth-death processes are subject to additional sources of process error (experiment # 2), (iii) is the PBR approach sufficient to enable populations to recover when there are catastrophic mortality events and trends in natural mortality (experiment # 2), and (iv) how will the PBR approach perform when multiple fisheries cause bycatch from the same populations of marine mammals but only some fisheries are managed (experiment # 3)? The impacts of the uncertainties are evaluated for two cetacean and two pinniped species, characterized by survival and maturation rates for the humpback whale and the bottlenose dolphin (cetaceans) and a fur seal and a sea lion (pinnipeds).

## Methods

### Overview

An MSE involves four steps: (i) identifying the management objectives and quantifying them using performance metrics, (ii) developing and parameterizing a set of operating models, (iii) identifying candidate management strategies, and (iv) projecting the populations represented within the operating models forward for each management strategy and computing performance metrics. The following sections outline (i) the operating model, (ii) the simulation experiments, which relate to the management strategies and how the operating model is specified, and (iii) the performance metrics that quantify the probability of recovery of depleted populations and the ability to maintain populations at MNPL if they are already at that level.

### Operating model

The operating model (Table 1) is an extension of the biological model developed by Punt *et al.* (2018). It is an integer-based, age- and sex-structured population dynamics model (T1.1). The expected number of progeny (pups or calves, depending on the

species) each year depends on the number of females that have reached the age of first parturition (T1.5) and a density-dependent birth rate where the extent of density dependence is a function of the abundance of animals aged 1 and older, relative to  $K^{1+}$  (carrying capacity, or the number of animals aged 1 and older at steady state if there had never been bycatch; T1.6). The operating model allows for demographic uncertainty (binomial probability, by age and sex, of being born or dying; T1.1 and T1.3). It also allows for environmental stochasticity in birth rates (normal error on the logit of the birth rate for cetaceans—which ensures that the birth rate never exceeds 1—and lognormal for pinnipeds, as the variation in birth rate for pinnipeds is confounded with variation in age-0 survival in the model; T1.4a and b) and 1+ survival rate (normal error on the logit of annual survival rate; T1.8). The expected value of (T1.8) is not the expected survival rate of animals of age  $a$ , so the value of  $\tilde{S}_a$  in (T1.8) is adjusted such that  $E(S_{t,a}) = \tilde{S}_a$  using a numerical search algorithm. The operating model allows the annual birth and death rates to be correlated (T1.9b). Autocorrelation in birth and death rates does not capture major mortality events [unusual mortality events (UMEs) as they are referred to in the United States] so the operating model includes the possibility that a “catastrophic event” occurs (with probability  $\Psi_C$ ) in which a proportion  $Q$  of all animals in the population dies. The impacts of large-scale forcing (such as climate change) could lead to increases in natural mortality over time, which is reflected in the operating model by a proportional decrease over time in  $\tilde{S}_a$ . Finally, the impacts of sublethal effects on expected birth rates are modelled by reducing the expected birth rate proportionally to the ratio of bycatch to population size (T1.6). This involves reducing the birth rate by  $(1 - \tau M_t / N_t^{1+})$  where  $M_t$  is the bycatch mortality,  $N_t^{1+}$  is the number of animals aged 1 and older, and  $\tau$  determines the strength of the sublethal effect (non-existent for  $\tau = 0$  and greater for higher values of  $\tau$ ).

To initiate the simulations, the number of animals by age and sex at carrying capacity (year  $-300$ ) is computed based on a pre-specified value for the number of aged 1+ animals ( $K^{1+}$ ), under the assumption that the population size is equal to carrying capacity and has a stable age-structure and an equal sex-ratio. The age and sex structure at the start of the first projection year (the first year in which the management system is applied; year 0) is computed by projecting the population forward to year 0 under a constant probability of being bycaught and solving for this probability,  $\bar{B}^f$  (i.e.  $B_t^f = \bar{B}^f$ ), so that the number of aged 1+ animals at the start of the first projection year relative to  $K^{1+}$  equals either 0.3 (depleted, according to the MMPA) or 0.5 (recovered or at MNPL).

The operating model assumes that there are several ( $N_f$ ) fishery-types  $f$  (i.e. fishing fleets using similar fishing practices in terms of bycatch risk to marine mammals), each of which causes bycatch mortality. Human-caused mortality is hence the sum over fishery types of the mortality by fishery type (T1.10). The fishery types are assumed to fish sequentially for computational ease, i.e. bycatch in fishery type 1 occurs first, followed by bycatch in fishery type 2, etc. (T1.11). All animals aged 1 and older are assumed to be equally vulnerable to bycatch, with calves/pups (i.e. animals  $<1$  year old) not being impacted directly [Studies (e.g. Brandon *et al.*, 2017) have shown that the results of long-term projections are not very sensitive to age-specific vulnerability, but that sex-bias towards females leads to lower rates of the recovery of depleted populations.]. Equation (T1.11) sets the fully

vulnerable removal rates (i.e. the removal rates of animals for which vulnerability is highest) by fishery type so that the overall cumulative removal rate is obtained given the sequential nature of the fishery types (T1.12). The realized bycatch mortality rate is beta-distributed about the expected rate with a C.V. of 0.3 [This mimics the assumption of Wade (1998) that realized catches are normally distributed about bycatch limits with a C.V. of 0.3]. The value of the PBR is updated each time a survey estimate of abundance becomes available.

The sampling error for the estimates of abundance is assumed to be lognormal (T1.13). Allowance is made for the possibility that there is a non-linear relationship between the expected value of the abundance estimate and true abundance; at  $c=0$ , the relationship is linear but for  $c>0$  the expected value of the abundance estimate declines slower than true abundance such that at  $c=1$  the expected abundance estimate is independent of true abundance. Non-linearity between an estimate of abundance and true abundance is not expected for well-designed surveys but could occur when density for a surveyed region is extrapolated to a population's entire geographic range and changes in population size do not occur uniformly across that range.

## Scenarios

The operating model is parameterized for two species of cetaceans and two species of pinnipeds (see Table 3 for the biological parameter values for each species). The maximum population growth rate  $\lambda_{MAX}$  is set to 1.04 for the cetaceans and 1.12 for the pinnipeds to match the assumptions of Wade (1998)—actual rates of increase for cetaceans and pinnipeds typically differ among species and populations within species (e.g. IWC, 2014 for cetaceans).  $\lambda_{MAX}$  is not varied here because the effects of this uncertainty are well known (e.g. Wade, 1998; Brandon et al., 2017; Punt et al., 2018). Table 3 does not specify values for the birth rate at unexploited equilibrium or in the limit of zero population size. These values are computed so the population is at equilibrium when  $N_t^{1+} = K^{1+}$  and so that the maximum rate of increase equals  $\lambda_{MAX}$ , respectively.

We conducted three simulation experiments. All experiments separately considered the four life history types, two levels for  $F_R$  (0.5 and 1.0), two levels for the ratio of initial aged 1+ abundance to  $K^{1+}$  (0.3 and 0.5), and two levels of  $K^{1+}$  (10 000 000 and 1000). The first of these levels for  $K^{1+}$  is unrealistic in most cases but was included to allow the effects of demographic stochasticity to be quantified (it will be minimal for a  $K^{1+}$  of 10 000 000 but perhaps consequential for a  $K^{1+}$  of 1000). For the ease of interpretation (and to keep the volume of results to a reasonable level), the experiments did not involve crossing all factors; for example, experiments # 1 and # 2 considered only a single fishery type (see Table 4 for the factors considered in each experiment and corresponding parameter values and Table 5 for the three experimental designs).

### Experiment # 1

This experiment explored the implications of assumptions regarding aspects of monitoring: the quality of available data, as characterized by the frequency with which surveys are undertaken; precision of the estimates of abundance; bias in estimates of abundance; and extent of non-linearity in the relationship between estimated and true abundance. The operating model included one fishery, demographic but not environmental

stochasticity and no catastrophic events and ignored the sublethal effects of bycatch.

The levels for survey frequency, survey precision and survey bias were based on those considered by Wade (1998), who explored the effects of each of these factors individually. Two levels for the extent of non-linearity  $c$  in (T1.13) were considered (a linear relationship,  $c=0$ ; and one in which estimated abundance declined more slowly than true abundance,  $c=0.5$ ). The latter relationship describes a case of survey bias where the survey cannot detect declines in abundance at the moment they occur, such as could occur when density does not initially decline in preferred core habitat areas (i.e. such as in the “Basin” model, MacCall, 1990). This type of survey bias was also considered in the tests of the Revised Management Procedure by the Scientific Committee of the International Whaling Commission with a similar size of effect (IWC, 1992), and a value of  $c=0.5$  provides a reasonable test of this type of survey bias.

### Experiment # 2

This experiment explored the implications of environmental stochasticity in birth and survival rates, catastrophic events, and sublethal effects. The magnitude of variation for these effects is hard to quantify for most pinnipeds and even more so for cetaceans because such quantification requires time-series of estimates of birth and survival, which are rare. However, such effects are plausible and have been observed for some marine mammal species (Supplementary S2). The values for the parameters governing environmental stochasticity and catastrophic events in the operating model (Table 4) were selected based on literature values, which are summarized in Supplementary S2. The estimates of variation in Supplementary Table S2.1 implicitly included measurement error as well as true variation in biological parameters. Consequently, the values in Table 4 were set to half of the point estimates and the highest values (central and upper values respectively) based on the literature values. Results are not shown for simulations that included autocorrelation between survival and birth rate because the empirical estimates of autocorrelation were low (Supplementary S2) and because the initial analyses with such autocorrelation (not shown) did not reveal this to be a major factor influencing the values for the performance metrics even when levels of autocorrelation far larger than those in Supplementary S2 were considered. The simulations with correlation between survival and birth rates were conducted for the central values for variation in survival and birth rates ( $\sigma_{Sa} = 0.6$ ;  $\sigma_b = 0.4$ ). There are almost no quantitative data on trends in natural mortality and sublethal effects for marine mammals, so the results for these trials need to be interpreted with more caution than those for other cases. The operating model included one fishery and a single monitoring scheme (4-year survey interval, abundance C.V. = 0.2, and a linear relationship between the estimates of abundance and true abundance).

The values in Table 4 cover a broad range because there are few data to inform their values and in general the time-series in Supplementary S2 are quite short. As such, the results should be considered to be exploratory rather than definitive, with the actual values likely varying among taxa and regions. The aim of the analyses was therefore primarily to learn about the relative importance of the factors considered.

The results of projections with environmental stochasticity can be hard to interpret so results are presented for both the case in

**Table 1.** The population dynamic equations underlying the operating model.

| Equation number     | Equation  | Description  |
|---------------------|---|--|
| Population dynamics |   |  |
| T1.1                | $N_{t+1,a}^s = \begin{cases} B(C_{t+1}, 0.5) & \text{if } a = 0 \\ B(N_{t,a-1}^s - M_{t,a-1}^s, S_{t,a-1}) \tilde{S}_t & \text{if } 1 \leq a < x \\ B(N_{t,x-1}^s - M_{t,x-1}^s, S_{t,x-1}) \tilde{S}_t + B(N_{t,x}^s - M_{t,x}^s, S_{t,x}) \tilde{S}_t & \text{if } a = x \end{cases}$ | Basic population dynamics                            |
| T1.2                | $B(z, p)$   | Binomial distribution with parameters $z$ and $p$    |
| T1.3                | $C_t = B(P_t, b_t)$   | Calf production                                      |
| T1.4a               | $b_t = \left(1 + \exp(\tilde{b}_t + \eta_t^b \sigma_b)\right)^{-1}; \tilde{b}_t = \ln(1/\tilde{b}_t - 1)$   | Stochastic birth rate (cetaceans)                    |
| T1.4b               | $b_t = \tilde{b}_t \exp(\eta_t^b \sigma_b - \sigma_b^2/2)$  | Stochastic birth rate (pinnipeds)                    |
| T1.5                | $P_t = \sum_{a=a_p}^x N_{t,a}^{\text{fem}}$   | Breeding females                                     |
| T1.6                | $\tilde{b}_t = b_{\text{eq}} \max\{0, 1 + (b_{\text{max}}/b_{\text{eq}} - 1)[1 - (N_t^{1+}/K^{1+})^\theta]\} \left(1 - \tau \frac{M_t}{N_t^{1+}}\right)$  | Density-dependent birth rate                         |
| T1.7                | $N_t^{1+} = \sum_{s=1}^x \sum_{a=1}^x N_{t,a}^s$  | Number of animals aged 1 and older                   |
| T1.8                | $S_{t,a} = \exp\left(\ln(1 + \exp(\tilde{S}_a + \eta_t^s \sigma_{sa})) e^{M_{t,a}}\right)$  | Annual survival by age                               |
| T1.9a               | $\eta_t^b \sim N(0; 1); \eta_t^s \sim N(0; 1)$  | Process errors in survival and birth rate            |
| T1.9b               | $\eta_t^b = \rho_{sb} \eta_t^s + \sqrt{1 - \rho_{sb}^2} \zeta_t; \zeta_t \sim N(0; 1)$  |  |
| T1.10               | $M_{t,a}^s = \sum_{f=1}^{N_j} M_{t,a}^{s,f}$  | Human-caused mortality by sex and age                |
| T1.11               | $M_{t,a}^{s,f} = B(N_{t,a}^s - \sum_{f'=1}^{f-1} M_{t,a}^{s,f'}, \phi_a^{s,f} \tilde{B}_t^f)$   | Human-caused mortality by sex, age, and fishery type |
| T1.12               | $\tilde{B}_t^f = B_t^f / (1 - \sum_{f'=1}^{f-1} B_{t'}^f)$  | Effective removal rate by fishery type               |
| Data generation     |   |  |
| T1.13               | $\hat{N}_t = \beta N_t^{1+} (K^{1+}/N_t^{1+})^c; e^{\epsilon_y - \sigma^2/2} \epsilon_y \sim N(0; \sigma_N^2)$  | Estimates of abundance                               |

Table 2 provides the definitions for the symbols.

which management was based on the PBR approach as well as when all human-caused removals are eliminated. Rather than combining all sources of uncertainty, each source was examined separately, which reduced the number of trials and eases interpretation of the results.

**Experiment # 3**

This experiment considered the implications of managing only one of two fisheries that bycatch animals incidentally from the same marine mammal population. The operating model contained two fisheries that impacted the same age and sex classes of animals but differed in terms of the proportion of the population that they affected. “Fishery 1” was nominally the fishery that exports to the United States and was always managed according to PBR. In this experiment, “Fishery 2” was not managed and three scenarios explored variation in the relative impact of each fishery on the marine mammal population (scenarios A–C in Table 4). The operating model included demographic uncertainty but not environmental stochasticity or catastrophic events, ignored the sublethal effects of bycatch, and assumed the same monitoring system as for experiment # 2.

**Performance metrics**

Following Wade (1998), Brandon et al. (2017) and Punt et al. (2018), conservation performance was evaluated using the following metrics:

- (i) The probability that the number of animals aged 1+ is greater than MNPL ( $0.5 K^{1+}$ ) after 100 years. For this calculation, MNPL is taken to be  $0.5 K^{1+}$ . Given the stochastic nature of births, deaths and reproduction in the operating model, the population will fluctuate about its carrying capacity in the absence of human-caused mortality rather than reaching and staying at that size.
- (ii) The lower fifth percentile of the ratio of the number of animals aged 1+ to  $K^{1+}$  after 100 years.

Wade (1998) identified a performance “standard” of a 95% probability of recovery to MNPL after 100 years for a population initially at  $0.3 K$  with an MNPL of  $0.5 K$ , and a 95% probability that a stock initially at  $0.5 K$  remains above  $0.5 K$  after 20 years. We also evaluated whether the lower fifth percentile of abundance after 100 years is at or above MNPL.

**Results**

Figure 1 shows time-trajectories of aged 1+ population size (medians and 90% intervals across simulations by year) and removals for eight trials for cetacean 1 (two values for  $F_R$ , two values for initial depletion, and two values for carrying capacity) from simulations based on a base-case set of specifications for monitoring, a single fishery, with no environmental variation. Three random individual replicate results are also provided to better indicate among-replicate variation. The eight trials pertain to experiment # 1 with a survey frequency of 4 years, and unbiased abundance estimates with a C.V. of 0.2.

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

| Symbol                     | Description  |
|----------------------------|--|
| $B_t^f$                    | Unconditional removal rate for fully vulnerable animals during year $t$ (i.e. the probability of a fully vulnerable animal being removed during year $t$ by fishery-type $f$ ) |
| $\tilde{B}_t^f$            | Removal rate for fully vulnerable animals that have survived fishery types $1, 2, \dots, f-1$  |
| $C_t$                      | Number of calves at the start of year $t$  |
| $K^{1+}$                   | Carrying capacity in terms of the number of animals aged 1 and older   |
| $M_t$                      | Human-caused mortality during year $t$   |
| $M_{t,a}^s$                | Human-caused mortality of animals of sex $s$ and age $a$ during year $t$   |
| $M_{t,a}^{s,f}$            | Human-caused mortality of animals of sex $s$ and age $a$ by fishery-type $f$ during year $t$   |
| $M_T$                      | Linear trend in natural mortality over time  |
| $N_f$                      | Number of fishery types  |
| $\tilde{N}_t$              | Estimate of the number $1+$ animals at the start of year $t$   |
| $N_{t,a}^s$                | Number of animals of age $a$ and sex $s$ (m/fem), at the start of year $t$   |
| $\tilde{N}_a^{\text{fem}}$ | Number of females if the number of calves is set to 1  |
| $N_t^{1+}$                 | Number of animals aged 1 and older at the start of year $t$  |
| $\Psi_C$                   | Probability of a catastrophic event  |
| $P_t$                      | Number of females that have reached the age of first parturition ( $a_p$ ) at the start of year $t$  |
| $Q$                        | Catastrophic survival ( $Q \leq 1$ ) $\tilde{S}_t = Q$ in catastrophic cases and 1 otherwise   |
| $\tilde{S}_a$              | Expected survival rate for animals of age $a$  |
| $S_{t,a}$                  | Survival rate for animals of age $a$ during year $t$   |
| $\tilde{S}_t$              | Annual survival multiplier [ $= Q$ with probability $\Psi_C$ or $\exp(-M_T t)$ for $t > 0$ ]   |
| $a_p$                      | Age-at-first parturition   |
| $b_t$                      | Birth rate during year $t$   |
| $\tilde{b}_t$              | Expected birth rate during year $t$  |
| $b_{\text{eq}}$            | Birth rate when the population is at carrying capacity; $b_{\text{eq}} = (\sum_{a=a_p}^s \tilde{N}_a^{\text{fem}})^{-1}$   |
| $b_{\text{max}}$           | Birth rate in the limit of zero population size  |
| $C$                        | Extent of saturation ( $c < 1$ ) in survey estimates of abundance  |
| $X$                        | Plus-group age (values for the population dynamics parameters, including human-caused mortality rates, are the same from age $x$ onwards)                                      |
| $\beta$                    | Extent of bias in the abundance estimate   |
| $\phi_a^{s,f}$             | Relative vulnerability of animals of age $a$ and sex $s$ to fishery-type $f$   |
| $\tau$                     | Extent of sublethal effects on birth rate  |
| $\rho_{sb}$                | Correlation between survival and birth rate  |
| $\theta$                   | Shape parameter, which determines where MNPL occurs relative to carrying capacity [computed from MNPL using the equations in Punt (1999)]                                      |
| $\sigma_N$                 | The standard error of the observation errors, i.e. $\sigma_N^2 = \ell n(1 + C.V._N^2)$ , where $C.V._N$ is the coefficient of variation about the true abundance               |
| $\sigma_b$                 | Standard deviation of the logit of birth rate  |
| $\sigma_{S_a}$             | Standard deviation of the logit of survival rate of animals of age $a$   |

As expected, the distributions for past and future population size depend on carrying capacity, with the results for the higher carrying capacity ( $K^{1+} = 10\,000\,000$ ) being almost deterministic (Figure 1a–d). The distributions for relative abundance are much broader for a  $K^{1+}$  of 1000 (Figure 1i–l). There is considerable variation in human-caused removals because this variation is driven

primarily by the precision of the estimates of abundance (Figure 1e–h and m–p), which is based on a C.V. of 0.2 for all of the simulations in Figure 1. Removals are reduced in year 0 for both levels of  $F_R$  when the population is initially at  $0.30 K^{1+}$  because the bycatch mortality prior to the first calculation of PBR exceeds PBR, as well as when  $F_R = 0.5$  and the population is initially at  $0.5 K^{1+}$ . However, and as expected, the reduction in removals is much greater for  $F_R = 0.5$  (Figure 1e, g, m, and o). The rate of recovery also depends on  $F_R$ , with recovery to MNPL occurring around year 45 for  $F_R = 0.5$ . Recovery probability for  $F_R = 1$  only reaches 0.4 when  $K^{1+} = 1000$  because of demographic uncertainty; in the nearly deterministic case, recovery does not occur, but the population size trajectories are close to MNPL at the end of the 100-year projection period and would reach MNPL after a few additional years (Figure 2).

### Experiment # 1

Figure 3 summarizes the results of experiment # 1 for cetacean 1 (see Supplementary Figure S3a–c for the remaining life histories). As expected, the value of  $F_R$  had the largest effect on the results, with recovery being achieved with at least 95% probability for most scenarios when  $F_R = 0.5$  and unbiased estimates of abundance, but much lower probabilities for the scenarios with an  $F_R$  of 1 or with a survey bias of 2 (Figure 3a). At the lower (more conservative) recovery factor and unbiased surveys, the only cases for which  $P(N^{1+} > \text{MNPL})$  was consistently  $< 0.95$  and the lower fifth percentile of abundance after 100 years was less than MNPL were when the survey C.V. was 0.8 and there was a non-linear relationship between the estimated and true abundance.

The second-largest effect came from the size of the survey bias (the ratio of expected estimated abundance to true abundance). A survey bias of 2 is essentially the same as doubling  $F_R$  so the results for  $F_R = 0.5$  and a survey bias of 2 were similar to those for  $F_R = 1$  and a survey bias of 1. However, conservation performance was very poor when  $F_R = 1$  and survey bias was 2, with a zero probability of being above MNPL after 100 years and a greater than 0.05 probability of 5% of populations being rendered extinct. A non-linear relationship between the expected estimate of abundance and true abundance ( $c = 0.5$ ), when there is a difference, led to a lower probability of achieving the recovery goal compared to when there was a linear relationship.

The results were relatively insensitive to the C.V. of the abundance estimates, although the lower fifth percentile of population size after 100 years was lower with a higher C.V. (Figure 3b). The results were also not very sensitive to survey frequency, although the probability of recovery after 100 years was generally higher when surveys were more frequent (except for the pinniped when  $F_R = 1$ ; see Supplementary Figure S3b and c). The effects of the overall magnitude of carrying capacity on the results were as expected from Brandon et al. (2017); i.e. recovery probability was lower for  $K^{1+} = 1000$  than for  $K^{1+} = 10\,000\,000$  for  $F_R = 0.5$ . The higher variability associated with a lower value for  $K^{1+}$  meant that the recovery probability was higher for the lower  $K^{1+}$  (Figure 3a), a result evident for the other experiments as well. The results for a population initially at  $0.5 K^{1+}$  were generally slightly more optimistic than those for a population initially at  $0.3 K^{1+}$ , but the relative performance among scenarios was similar across initial depletion levels. Results are consequently only reported for an initial population size of  $0.3 K^{1+}$  for the remaining simulation experiments.

**Table 3.** The values for the biological and fishery parameters of the operating model.

| Parameter                                 | Pinniped 1  | Pinniped 2                         | Cetacean 1                             | Cetacean 2                              |
|---|---|------------------------------------|--|---|
| Age-at-first parturition, $a_p$           | 4 years   | 5 years                            | 5 years (Zerbini <i>et al.</i> , 2010) | 7 years <sup>a</sup>                    |
| Calf/pup survival rate, $S_0$             | 0.77  | 0.83                               | 0.90 (Zerbini <i>et al.</i> , 2010)    | 0.865 (Arso Civil <i>et al.</i> , 2019) |
| Adult survival rate, $S_a$ ( $a > 0$ )    | 0.88 [(Butterworth <i>et al.</i> , 1995 cited in Wickens and York (1997)] | 0.95 (DeLong <i>et al.</i> , 2017) | 0.95 (Zerbini <i>et al.</i> , 2010)    | 0.951 (Speakman <i>et al.</i> , 2010)   |
| Vulnerability                             | Age 1+  | Age 1+                             | Age 1+                                 | Age 1+                                  |
| Plus-group age                            | Age 10  | Age 5                              | Age 15                                 | Age 10                                  |
| Maximum rate of increase, $\lambda_{max}$ | 1.12  | 1.12                               | 1.04                                   | 1.04                                    |

The biological parameters (age-at-first parturition, calf survival rate, and adult survival rate) for the two cetaceans are represented by a baleen whale (characterized by the humpback whale *Megaptera novaeangliae*) and a toothed whale (characterized by the common bottlenose dolphin *Tursiops truncatus*). The two pinniped species are represented by a fur seal (characterized by the Cape fur seal *Arctocephalus pusillus*) and a sea lion (characterized by the California sea lion *Eumetopias jubatus*). Life histories for these characteristic species are re-scaled for performance-testing purposes, to have the same maximum growth rate values as assumed by Wade (1998): 1.04 for cetaceans and 1.12 for pinnipeds.

<sup>a</sup>Value selected given the wide range of values reported in the literature (e.g. Stolen and Barlow, 2003; Wells, 2003; Fruet *et al.*, 2015; a review by Vollmer and Rosel, 2013).

**Table 4.** Factors considered in the analyses.

| Factor  | Levels   |                            |     |
|---|--|----------------------------|-----|
| Population dynamic related  |  |                            |     |
| Species types   | Pinniped-1, Pinniped-2, Cetacean-1, Cetacean-2   |                            |     |
| Carrying capacity, $K^{1+}$   | 1 000, 100 00 000  |                            |     |
| Initial depletion, $\chi$   | 0.3, 0.5   |                            |     |
| Maximum rate of increase, $\lambda_{max}$   | 1.04 (whales), 1.12 (pinnipeds)  |                            |     |
| MNPL  | <b>0.5</b>   |                            |     |
| C.V. of fishing mortality, C.V. <sup>f</sup>  | <b>0.3</b>   |                            |     |
| Trends in natural mortality rate, $M_T$   | <b>0</b> , 0.005, 0.01   |                            |     |
| Variation in survival rate, $\sigma_{Sa}$   | <b>0</b> , 0.6, 1.3 (see Supplementary Figure S1 for the implied distributions for survival) |                            |     |
| Variation in birth rate, $\sigma_b$   | <b>0</b> , 0.4, 0.5  |                            |     |
| Probability of a catastrophic event, $\Psi_C$   | <b>0</b> , 0.05, 0.1   |                            |     |
| Extent of a catastrophic event on survival, Q   | <b>1</b> , 0.9, 0.5  |                            |     |
| Sublethal multiplier, $\lambda$   | <b>1</b> , 0.2, 0.01   |                            |     |
| Correlation between birth and survival rates, $\rho_{Sb}$   | <b>0</b> , 0.707, 0.9 ( $\sigma_{Sa} = 0.6$ ; $\sigma_b = 0.4$ )                             |                            |     |
| Fishery structure and impact  |  |                            |     |
| Number of fishery types   | <b>1, 2</b>  |                            |     |
| Scenarios regarding allocation of human-caused mortality to fishery type, $\Omega^f$              | Scenario   | Relative fishing mortality |     |
|   |  | 1                          | 2   |
|   | A  | 0.7                        | 0.3 |
|   | B  | 0.5                        | 0.5 |
|   | C  | 0.3                        | 0.7 |
| Monitoring  |  |                            |     |
| Frequency with which abundance estimates become available and allowable bycatch/PBR is calculated | <b>4, 8</b> years  |                            |     |
| Abundance estimate C.V.   | <b>0.2, 0.8</b>  |                            |     |
| Abundance estimate bias, $\beta$  | <b>1, 2</b>  |                            |     |
| Extent of density dependence in estimates, c  | <b>0.5, 0</b>  |                            |     |
| Management rules  |  |                            |     |
| Recovery factor, $F_R$  | 0.5, 1.0   |                            |     |
| Fishery-type 2 removals   | <b>Managed</b> , constant bycatch mortality rate, constant removal                           |                            |     |

The values in bold are the reference values [i.e. values in the studies by Wade (1998)].

**Table 5.** The scenarios considered in the analyses.

| Factor   | Experiment        |  |  |
|--|-------------------|--|--|
|  | 1                 | 2  | 3  |
| Population dynamic related                                 |                   |  |  |
| Species  | All               | All  | All  |
| Carrying capacity  | 10 000 000; 1 000 | 10 000 000; 1 000  | 100 000 000; 1 000   |
| Initial depletion  | 0.3, 0.5          | 0.3, 0.5   | 0.3, 0.5   |
| $\lambda_{\max}$   | 1.04/1.12         | 1.04/1.12  | 1.04/1.12  |
| Trend in natural mortality rate                            | 0                 | 0, 0.005, 0.01   | 0  |
| Variation in survival rate, $\sigma_{sa}$                  | 0                 | 0, 0.6, 1.4  | 0  |
| Variation in birth rate, $\sigma_b$                        | 0                 | 0, 0.4, 0.5  | 0  |
| Probability and (extent) of a catastrophic event, $\Psi_C$ | 0 (0)             | 0 (0), 0.1 (0.5), 0.05 (0.9)                             | 0 (0)  |
| Sublethal multiplier, $\lambda$                            | 1                 | 1, 0.2, 0.01   | 1  |
| Correlation between birth and survival rates, $\rho_{sb}$  | 0                 | 0, 0.707, 0.9 ( $\sigma_{sa} = 0.6$ ; $\sigma_b = 0.4$ ) | 0  |
| Fishery structure and impact                               |                   |  |  |
| Number of fishery types                                    | 1                 | 1  | 2  |
| Allocation scenarios                                       | N/A               | N/A  | A–C  |
| Monitoring   |                   |  |  |
| Frequency with which abundance estimates become available  | 4, 8              | 4  | 4  |
| Abundance estimate C.V.                                    | 0.2, 0.8          | 0.2  | 0.2  |
| Abundance estimate bias, $\beta$                           | 1, 2              | 1  | 1  |
| Survey non-linearity                                       | 0, 0.5            | 0  | 0  |
| Management rules   |                   |  |  |
| Recovery factor ( $F_R$ )                                  | 0.5, 1.0          | 0.5, 1.0   | 0.5, 1.0   |
| Fishery-type 2   | N/A               | N/A  | Managed, constant bycatch mortality rate, constant bycatch |
| Cases  | 512               | 416  | 288  |

Each experiment consisted of 1 000 replicates over 100 years for each trial. For definitions of “All”, see Table 3.

Figure 4 shows results for all four life history types for  $K^{1+} = 1000$  and the two survey frequencies. The qualitative effects of survey C.V., survey bias and the form of the relationship between the abundance estimates and true abundance were the same for all life history types (see Supplementary Figure S3a–c for the full set of results). However, the values for the performance metrics depended on life history. For example, the lower fifth percentiles of population size after 100 years for the two cetaceans (columns 1–4) were mostly higher than those for the two pinnipeds (columns 5–8) for the higher C.V.s.

## Experiment # 2

Several of the factors considered in experiment # 2 (see Table 5) were highly influential in terms of recovery probability and the lower fifth percentile of population size after 100 years (Figure 5). In particular, an increasing rate of natural mortality led to much lower rates of recovery even for  $F_R = 0.5$ , but the rates of recovery would be low even in the absence of bycatch (results not shown).

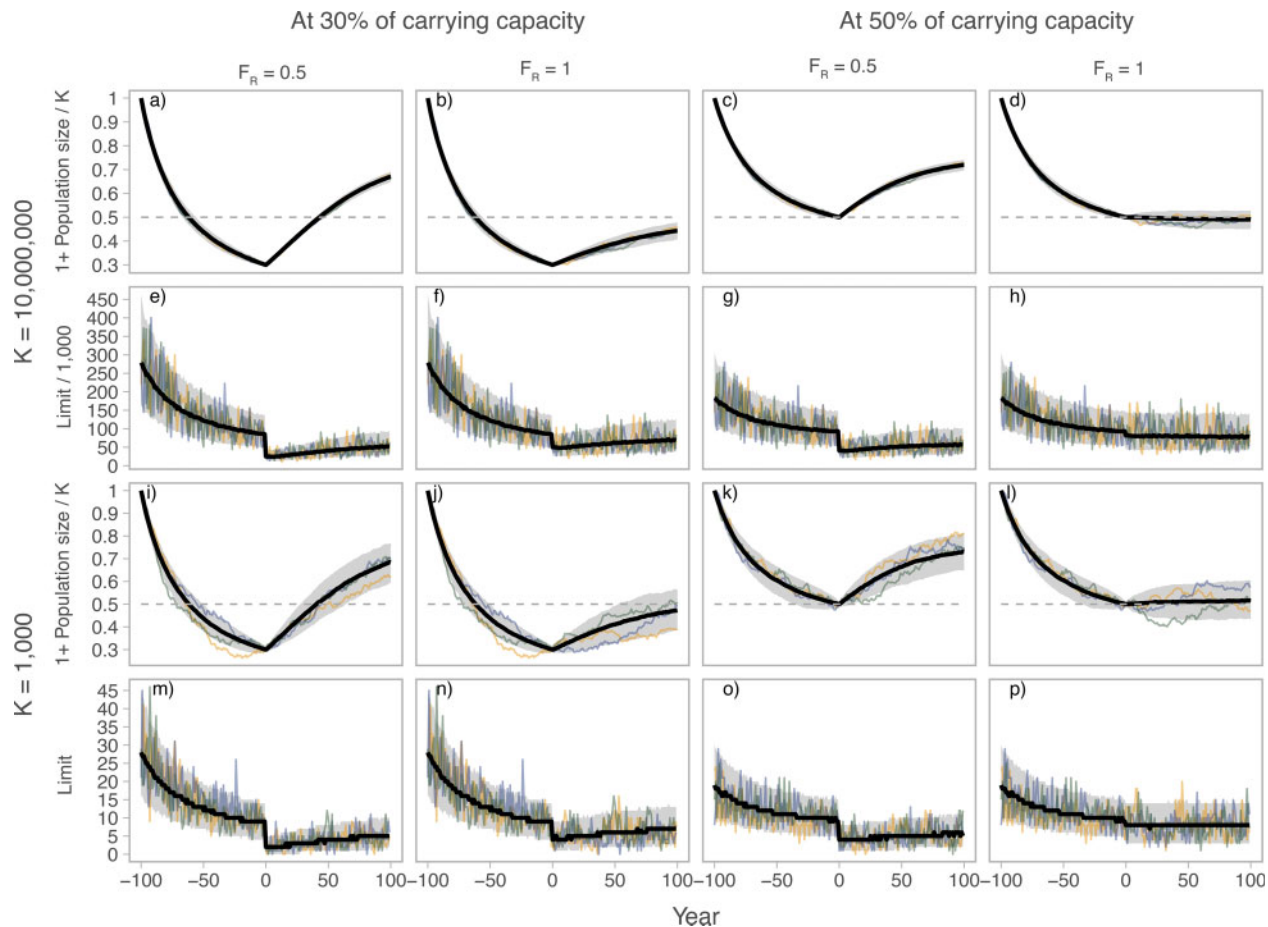
Catastrophic events that reduced the population by 50% with probability 0.1 reduced recovery probability to near zero for both life histories. As expected, effects of catastrophic events that reduced the population by 90% with probability 0.05 were less severe than those that reduced the population by 50% with probability 0.1. The effects of catastrophic events on recovery probability were slightly more marked for pinnipeds than cetaceans and adopting  $F_R = 0.5$  provided some robustness against catastrophic events.

Environmental variation in survival rates reduced recovery rates, with the effect of  $\sigma_{sa} = 1.3$  being quite substantial, particularly for the pinniped (e.g. Figure 5a–B and b–B). The probability of rebuilding was higher for the cetacean when there was variation in survival,  $K^{1+} = 10\,000\,000$  and  $F_R = 1$ , but this was because the recovery probability was zero for the baseline values for the parameters of the operating model. The effects of environmental variation in survival reduced the probability of recovery and the lower fifth percentile of population size after 100 years even in the absence of bycatch (Figure 6), but there were cases in which a no-bycatch mortality scenario led to a greater than 95% probability of being above MNPL after 100 years, whereas the same could not be achieved with a PBR approach recovery factor of  $F_R = 0.5$ . Using a PBR approach with  $F_R = 0.5$  could achieve similar recovery probabilities to a no-bycatch scenario for all life history types except pinniped 1 when survival variation was low ( $\sigma_{sa} < 1.3$ ; Figure 6).

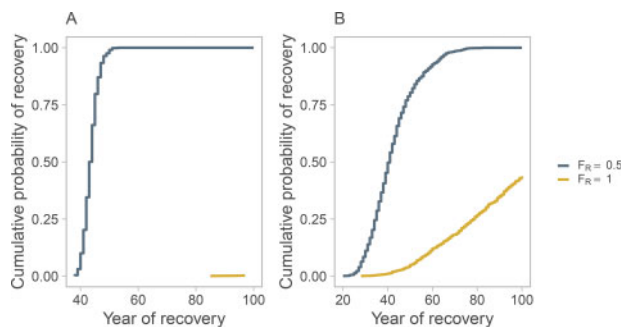
In general, recovery rates for pinniped life histories were more sensitive than cetacean life histories to higher trends in natural mortality, variation in survival and variation in birth rate, whereas catastrophic events appeared to have a stronger effect on cetacean recovery probabilities than pinniped recovery probabilities.

Variation in birth rates led to lower recovery rates and probabilities of being above MNPL, but the size of the effect (given the chosen parameter values) was less than for environmental variation in survival. As before, the probability of being above MNPL was higher for the cetaceans when there was environmental variation and  $F_R = 1$ , but this effect was evident for both levels of  $K^{1+}$ . Sublethal effects, at least as modelled in this article, had relatively





**Figure 1.** Results of projections (population size, first and third rows of panels; removals, second and fourth rows of panels) for eight trials for cetacean 1 [two levels for carrying capacity ( $K^{1+}$ ), two values for  $F_R$ , and two values for initial depletion]. The solid black line is the median, and the shading covers 90% of the distributions. Also, shown are trajectories from three individual replicates.



**Figure 2.** Cumulative probability of recovery for the scenarios in Figure 1 that start the projections from  $0.3 K^{1+}$ . Results are shown for (a) a carrying capacity of 10 000 000 and (b) a carrying capacity of 1000.

small effects on recovery probability as did correlations between the deviations in birth and survival rates.

**Experiment # 3**

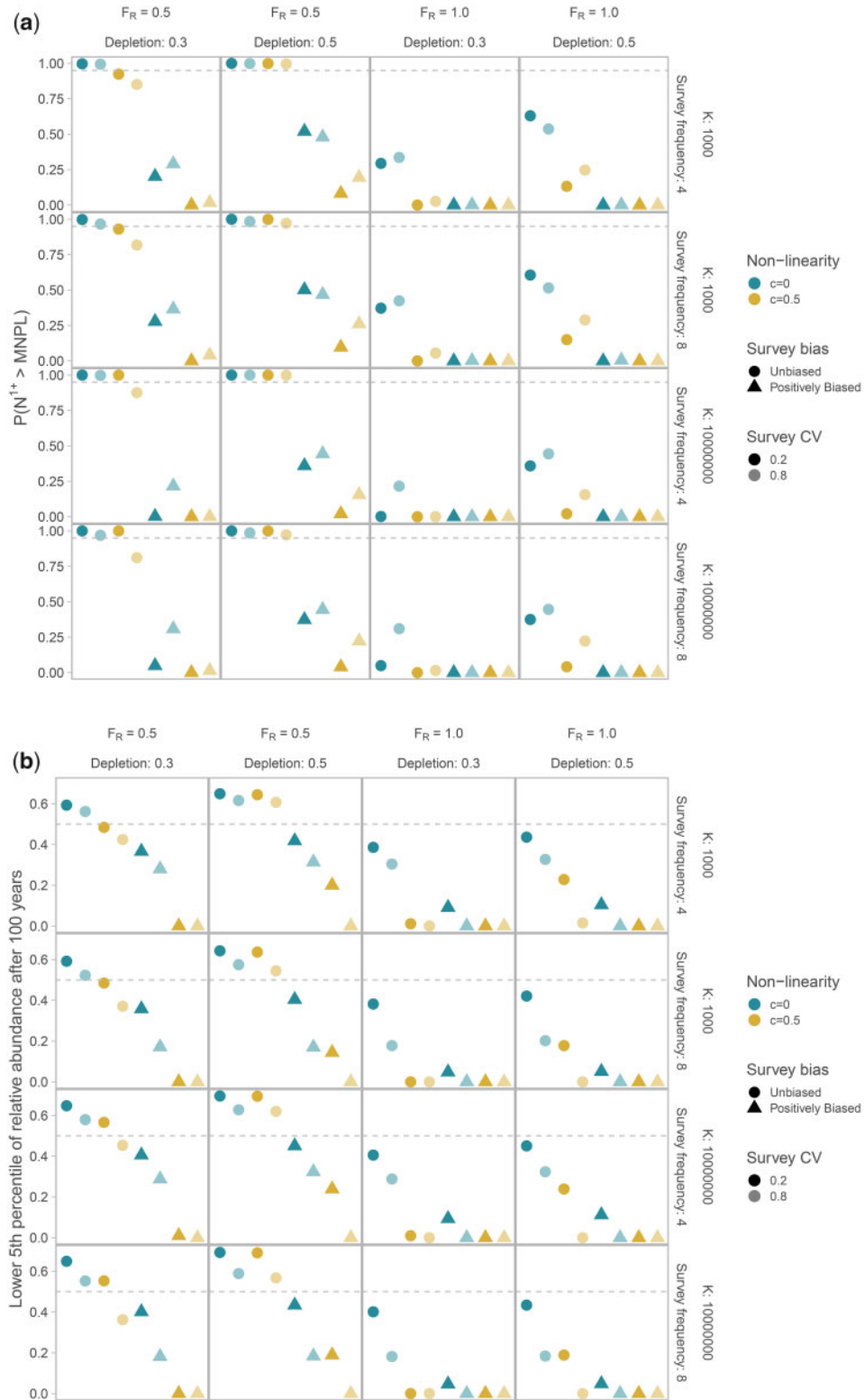
Figure 7 shows the results for experiment # 3 for the four life histories. As expected, conservation performance was almost always

poorer if there were two fisheries and only one was managed (blue points vs. brown points) and negative consequences were greater for scenario C (where the unmanaged fishery had a greater bycatch mortality rate than the managed fishery). The exception to this conclusion was the probability of rebuilding with  $F_R = 1$  when removal of a constant number of animals by fishery 2 led to higher values for the performance metrics (in some cases not managing a second fishery that removes a constant number of animals actually led to better conservation outcomes because the PBR approach allowed bycatch mortality to increase as the population recovered). In contrast, the lower fifth percentile of population size after 100 years was always lower when the unmanaged fishery removed a constant number of animals for the cetaceans. Removing a constant number of animals led to higher values of the lower fifth percentile of population size after 100 years for the pinnipeds when  $F_R = 0.5$ , except in scenario C.

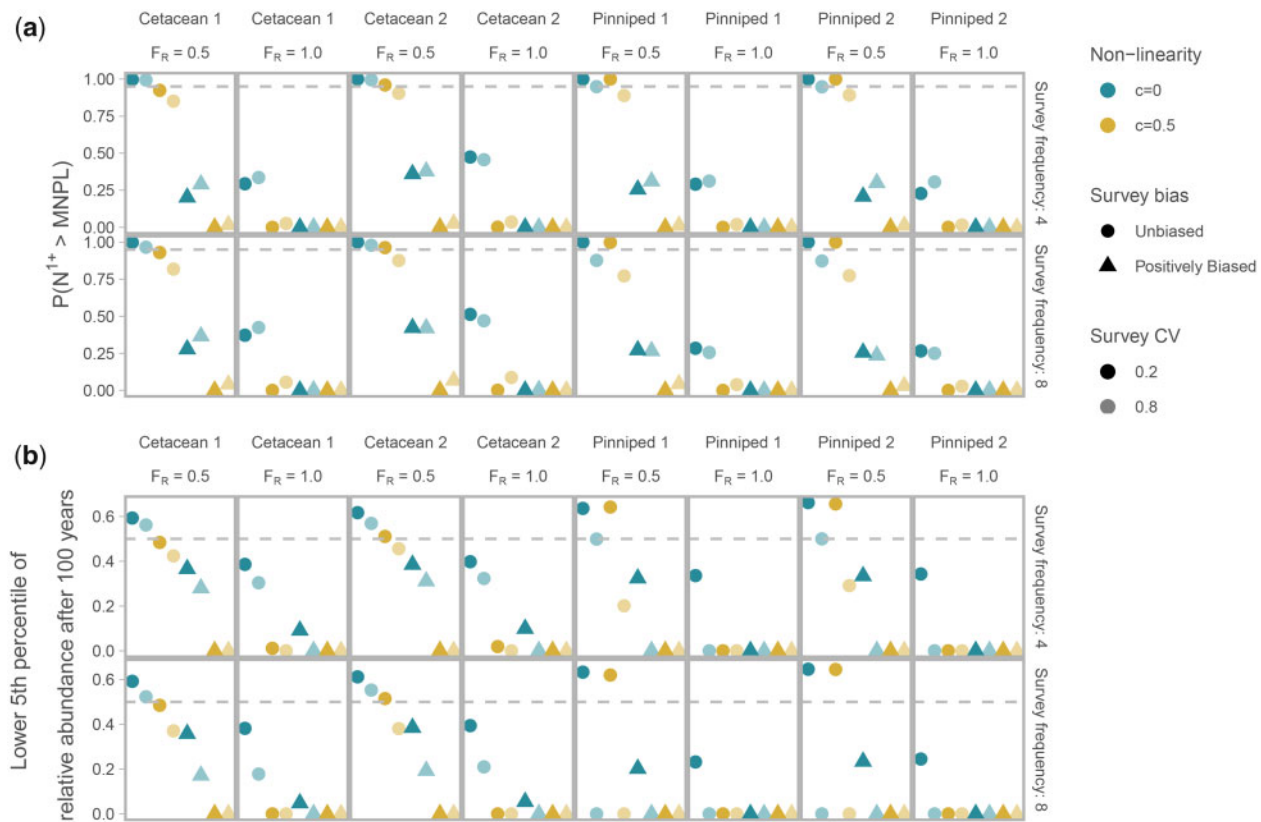
**Discussion**

**Overview of results**

The results presented here confirm previous results showing that how populations and fisheries are monitored is consequential for recovery when applying the PBR approach. They also confirm the results of Punt et al. (2018) that recovery probability depends to some extent on species life history, owing to demographic



**Figure 3.** Summary of the results of experiment # 1 for cetacean 1 according to two performance metrics: (a) the probability that the number of 1+ animals exceeds MNPL after 100 years and (b) the lower fifth percentile of the relative abundance ( $N^{1+}/K^{1+}$ ) after 100 years. Results are given for when the population is initially at 30% (depletion = 0.3, first and third columns) and 50% (depletion = 0.5, second and fourth columns) of carrying capacity. Results are shown for two values of  $F_R$  (0.5 and 1, columns 1–2 and 3–4, respectively), two values for carrying capacity ( $K^{1+} = 1000$  and  $10\,000\,000$ , rows 1–2 and 3–4, respectively), and eight scenarios regarding future monitoring including survey frequency (every 4 years, first and third rows; every 8 years, second and fourth rows), linearity between estimated and true abundance, and survey C.V. and bias (see legend for symbols). The horizontal lines are MNPL (a) and 0.95 (b).



**Figure 4.** Comparison of the results of experiment # 1 among the life history types (left four columns: cetaceans; right four columns: pinnipeds). The results for each life history type pertain to the case in which  $K^{1+} = 1000$  and the population is initially at a depletion of 0.30  $K^{1+}$ . The performance metrics for each analysis are: (a) the probability that the number of 1+ animals exceeds MNPL after 100 years and (b) the lower fifth percentile of the relative abundance ( $N^{1+}/K^{1+}$ ) after 100 years. The horizontal lines are MNPL and 0.95.

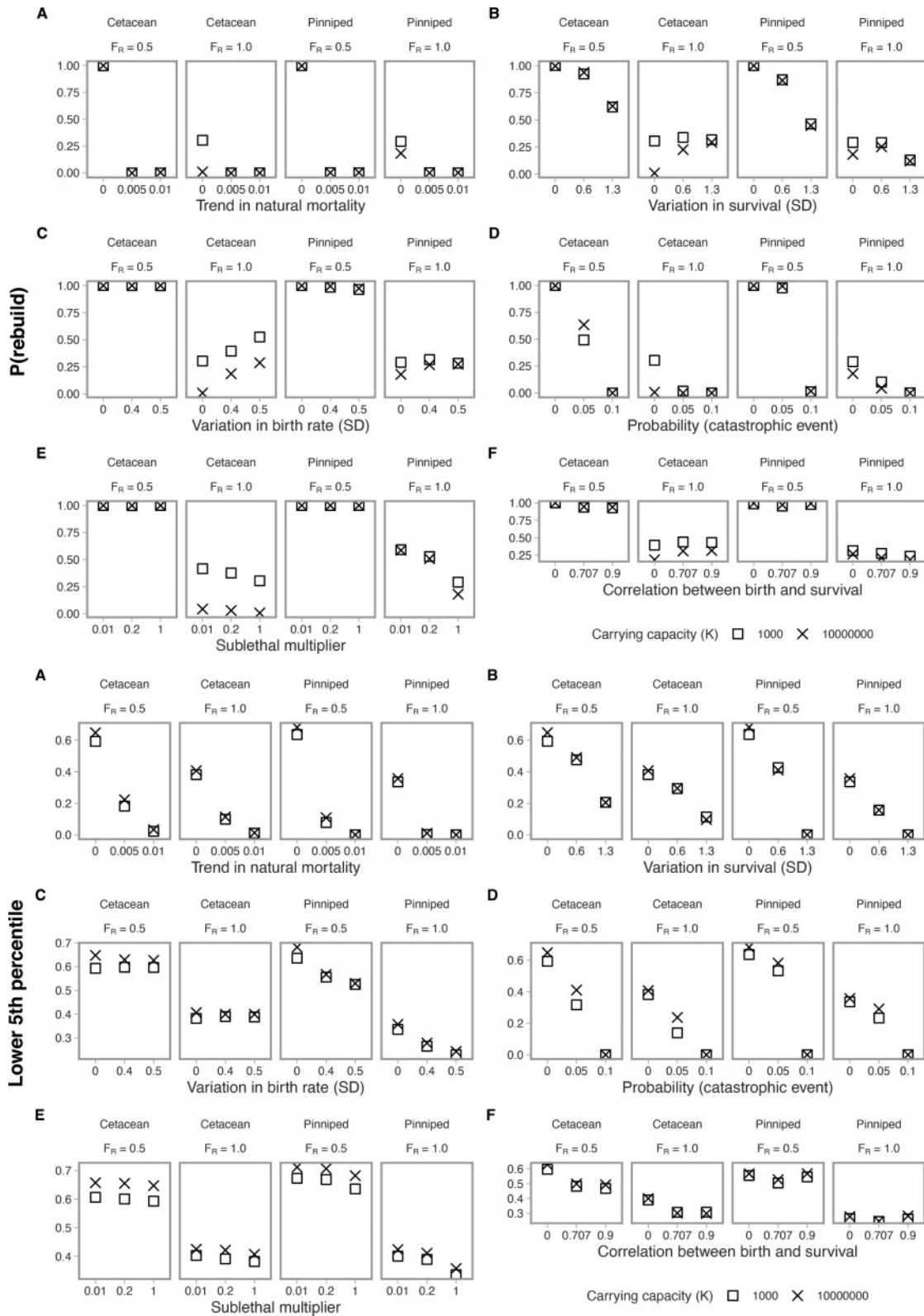
stochasticity and transient age-structure effects. Of the factors related to monitoring, survey bias is clearly the strongest reason for an inability to achieve management goals (see experiment # 1) and is one reason that  $F_R = 0.5$  was originally identified as a way to address the effect of uncertainties (Barlow *et al.*, 1995; Wade, 1998). The precision (C.V.) of the abundance estimates has a larger effect on the two pinnipeds, confirming the expectation that species with faster dynamics require more frequent monitoring.

The impact of variation in survival rate on recovery rate is much greater than of variation in birth rate, because variation in survival rate impacts all age-classes simultaneously, whereas variation in the birth rate impacts only a single age-class. In theory, temporal autocorrelation in survival and birth rate compounds the effects of variation, but the degree of autocorrelation found in existing studies (Supplementary S2) is not high enough to have a major effect on performance.

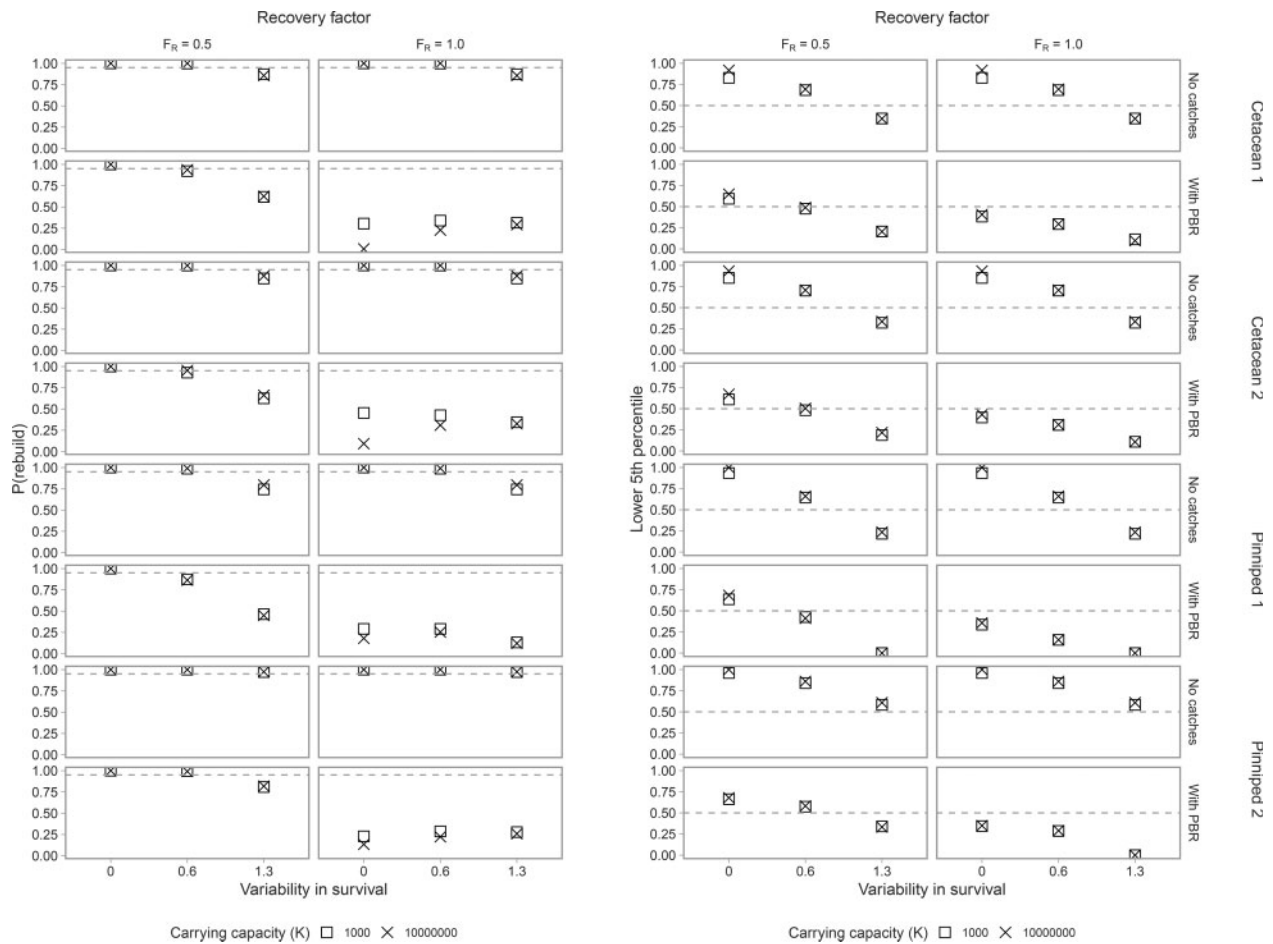
As expected, managing bycatch mortality in only one of the two fisheries that impact a marine mammal population (experiment # 3) leads to lower rates of recovery for depleted populations and lower probabilities of maintaining populations at MNPL, with constant removals due to bycatch generally having a major impact on these rates and probabilities. However, for most cases, managing at least one of multiple fleets that impacts a marine mammal population using the PBR approach has conservation benefits, although clearly not to the extent that would be the case if all fleets were managed.

### Implications for PBR management

The intent of the US Congress in adding  $F_R$  (with a possible range from 0.1 to 1.0) to the definition of PBR in the US MMPA was to ensure the recovery of populations to their optimum sustainable population levels and to ensure that the time necessary for populations listed as endangered, threatened, and/or depleted to recover was not significantly increased. This article does not address the special issue of endangered or threatened species but addressed the issue of whether depleted populations recover, and how quickly. The use of  $F_R < 1.0$  allocates a proportion of expected net production towards population growth and compensates for uncertainties that might prevent population recovery, such as biases in the estimation of  $N_{MIN}$  and  $R_{MAX}$ . Within the PBR context, the choice of  $F_R = 0.5$  as a default is intended as a precautionary buffer against the uncertainties originally considered by Wade (1998). This value is used as a default for populations that are depleted, threatened, or of unknown status, with the value allowed to be increased up to 1.0 when populations are well studied and biases in estimation of  $N_{MIN}$  and other parameters are thought to be negligible (Anon, 2016). Punt *et al.* (2018) found that transient age-structure effects lead to lower rates of recovery compared to the generalized logistic model on which the analyses of Wade (1998) were based, but that PBR management using  $F_R = 0.5$  still leads to the recovery of depleted populations, albeit at a slightly slower rate. Our results are broadly similar



**Figure 5.** Summary of the results of experiment # 2 for cetacean 1 and pinniped 1 when the population is initially at  $0.30 K^{1+}$ . The performance metrics for each analysis are: the probability that the number of 1+ animals exceeds MNPL after 100 years [ $P(\text{rebuild})$ ], and the lower fifth percentile of the relative abundance after 100 years (i.e. “lower fifth percentile”). The scenarios are (A) increasing trends in natural mortality; (B) increasing variation in survival; (C) increasing variability in birth rate; (D) increasing probability of a catastrophic event; (E) increasing strength of sublethal effects; and (F) increasing correlation between birth and survival. Descriptions of the values used in each case are found in Table 5.



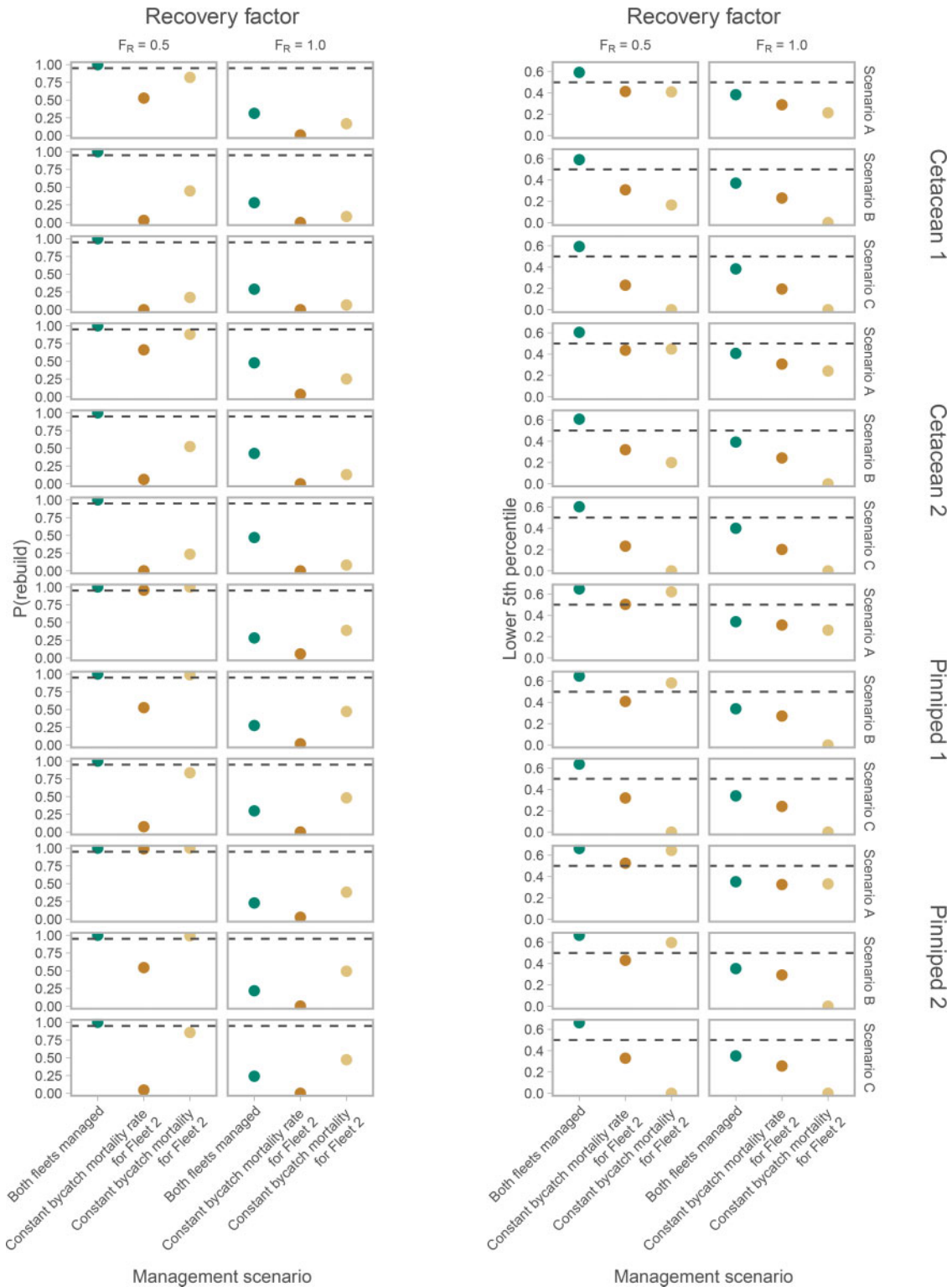
**Figure 6.** Comparison of the results of the simulations in which there is variation ( $\sigma_{sa}$ ) in survival rate among the life history types. The upper row for each life history type is when bycatch mortality is zero for all years, and the lower row for each life history type is when management is based on the PBR approach. The performance metrics for each analysis are the probability that the number of 1+ animals exceeds MNPL after 100 years [ $P(\text{rebuild})$ ] and the lower fifth percentile of the relative abundance ( $N^{1+}/K^{1+}$ ) after 100 years. The horizontal lines are 0.95 and MNPL.

here; when the management scheme is challenged by various scenarios, the use of  $F_R = 0.5$  often leads to achieving the management objective, or at least being much closer than would be the case when using  $F_R = 1.0$ , but there are important exceptions, discussed below. The US guidelines also allow for  $F_R$  to be adjusted to accommodate additional information and to allow for management discretion as appropriate and consistent with the goals of the MMPA, such as decreasing the value of  $F_R$  for cases where bycatch mortality is skewed towards reproductive females, or where the population is known to be declining. We make a similar recommendation regarding use of a lower value of  $F_R$  for another scenario (see below).

The results indicate that some sources of mortality (sublethal effects) at realistic levels may be managed via the PBR approach, but other sources of mortality (e.g. UMEs) can cause population collapses regardless of bycatch levels. The results of experiment # 2 should be interpreted in the context of how population size changed even if there was no bycatch. For example, there is a high probability of population collapse for the most rapid increase in natural mortality simulated here, irrespective of whether bycatch occurs. This demonstrates that UMEs can lead to collapses even in populations in which bycatch is tightly managed and confirm

that PBR management cannot, and should not, be expected to address uncertainties such as catastrophic events and decreasing survival rates due to factors other than bycatch mortality. However, given declining populations, the PBR formula reduces the limit on human-caused mortality, and if a major reduction in population size was to be detected, this could trigger a proportional downward adjustment in the value of  $F_R$ , at least as the PBR approach is applied in the United States.

The parameter values of the operating model for experiment # 2 reflect scenarios in which analyses are based on fairly limited data, particularly in relation to sublethal effects and catastrophes, and should be interpreted in that context rather than as estimates for particular populations or regions. Nevertheless, the results for experiment # 2 illustrate some possible consequences for marine mammal populations when the assumptions of the PBR approach are violated. Although sublethal effects for cetaceans and pinnipeds may be mitigated via the PBR approach, populations with catastrophic mortality events will not recover even if bycatch does not occur. These results suggest that comprehensive conservation plans should include bycatch as well as other potential threats and limits to bycatch alone may not be sufficient for improving population status.



**Figure 7.** Summary of the results of experiment # 3 for the four life history types when the population is initially at  $0.3 K^{1+}$  and  $K^{1+} = 1000$ . The horizontal lines are 0.95 and MNPL. Scenarios A, B, and C are explained in Table 4.

When a marine mammal population is subject to bycatch in multiple fisheries, only some of which are managed, the probability of recovery and maintaining the population at MNPL is lower and the performance goals are not achieved. However, this is to

be expected given that the PBR approach was not designed to address situations where some portion of the human-caused mortality is unmanaged. The modelling in the present study was motivated to reflect multiple fisheries in a country where only

some of the fisheries of concern are managed, but experiment # 3 could also be viewed as reflecting the situation of a population physically distributed between multiple countries, only one of which is managing bycatch mortality using the PBR approach. These results have consequences for expectations about the implementation and potential conservation benefits of the Seafood Import Rule.

The results presented here are not particularly sensitive to environmental variation in birth rates (our results are based on independent perturbations in birth rates, but with very similar results when there is autocorrelation in or among these perturbations). However, this was not the case for environmental variation in survival rate. Specifically, the probability of recovery and the lower fifth percentile of population size after 100 years did not achieve the “performance standard” of 0.95 of MNPL with PBR management and  $F_R = 0.5$  owing to the effects of transient age-structure effects and the time-lag inherent in age-structured population dynamics models (unlike the operating model of Wade, 1998). The performance standard would theoretically have been possible with a lower value of  $F_R$ , suggesting that there is capacity in the PBR approach to buffer against this type of variation. Environmental variation in survival rate is plausible and has been demonstrated for cetaceans and pinnipeds based on existing data (Supplementary S2). Consideration should be given to using a lower value of  $F_R$  for species for which there is evidence of considerable variation in survival rates.

### Future work

This article explored scenarios that can affect the performance of the PBR approach, expanding upon the analyses conducted by Wade (1998), Brandon *et al.* (2017) and Punt *et al.* (2018). We see some key directions for future work. The first is to further refine the scenarios for the parameters of the operating model. The results of the scenarios tested here were particularly sensitive to trends in natural mortality and were not sensitive to sublethal effects that reduce the birth rate. However, the parameter values governing these scenarios were largely guesses in the absence of empirical data. Had there been a weaker trend in natural mortality and had the magnitude of sublethal effects been substantially higher, the conclusions regarding which factor is more important could have been reversed. Risk-based assessments of how changes in natural mortality affect these populations should consider the relative impacts of these two scenarios.

The second direction for future work is to uncover and standardize additional empirical data on time-varying processes so that more realistic scenarios related to biological variation can be included in future MSEs for marine mammals. The parameter values for environmental variation in birth and survival rates are based on the published information presented in Supplementary S2. Field studies examining temporal variation and trends in natural mortality will eventually improve the ability to identify what recovery trajectories might be under the PBR approach or similar approaches. However, in the short term, it is likely that more time-series exist that could have been analysed, but they are not published for the species included in this study, or the results are not expressed in units that make the series fully comparable. As such, an effort to collate time-series of birth and survival rates for cetaceans and pinnipeds should be undertaken.

A rigorous review of time-varying life history characteristics should involve a hierarchical analysis that uses data from more

data-rich populations to estimate life history parameter values for data-poor populations (see Trukhanova *et al.*, 2018 who used such a method to estimate natural mortality for phocid seals). The sublethal effects of entanglement (including infection, “debilitation” and other factors that can influence long-term survival or reproduction) have been recorded in pinnipeds (Fowler, 1987), common bottlenose dolphins (*Tursiops truncatus*; Wells *et al.*, 2008; Barco *et al.*, 2010), and baleen whales (Cassoff *et al.*, 2011). Energetic costs related to entanglement have been quantified by van der Hoop *et al.* (2016a, b) and others. However, these effects have yet to be related quantitatively to likely impacts on demographic parameters such as birth rates to enable them to be included in models such as the operating model of this article.

The article does not explore all possible factors that could impact the performance of the PBR approach. For example, unlike Brandon *et al.* (2017), we do not evaluate alternative vulnerability patterns such as bycatch mortality being directed primarily at juvenile animals or pups/calves, and that mortality of a female with a calf/pup will lead to the death of that calf/pup. In addition, while environmental stochasticity in birth and death processes means that carrying capacity is no longer a static concept, the operating model does not consider long-term cycles in carrying capacity. This could be examined by either forcing trends in carrying capacity or considering an operating model with selection-delayed growth (e.g. Witting, 1997, 2003).

The simulations are based on “generic” species (archetypes), using reasonably well-known biological parameters of humpback whales, common bottlenose dolphins, a fur seal, and a sea lion. There may be value in conducting case-specific simulations for some populations for which more detailed biological data are available. In particular, the simulations are based on the default values for the maximum population growth rate  $\lambda_{MAX}$  (1.04 for cetaceans and 1.12 for pinnipeds). This parameter is poorly known for many species, but where available, alternatives could be specified and used in simulations [e.g. maximum rates of increase are higher for several humpback whale and southern right whale (*Eubalaena australis*) populations than the PBR default; IWC, 2014].

Finally, this article has evaluated the PBR approach. This approach has relatively limited data requirements. It would be expected that management strategies that are based on additional sources of data (e.g. time-series of removals and relative and absolute abundance, demographic parameters) would outperform the PBR approach. Simulations similar to those in which this article is based could be used to evaluate the performance of such strategies. For example, the Scientific Committee of the International Whaling Commission has evaluated management strategies tailored to harvesting by commercial and aboriginal subsistence whaling that use more data than the PBR approach (e.g. IWC, 2003, 2005, 2012).

### Conclusion

The current values of the parameters in the PBR formula lead to robustness to several sources of uncertainty, but this article shows that PBR management cannot guarantee that the conservation and management goals of the MMPA will be achieved when, for example, natural mortality increases for reasons unrelated to bycatch, unless the recovery factor  $F_R$  is reduced substantially (and perhaps not at all). Of the factors considered, environmental variation in survival rate had an appreciable effect on performance

while variation in birth rate did not. The quality (bias in particular) and frequency of monitoring efforts impacted the likelihood of achieving conservation objectives. Performance also varied by life history type, and depended on how many fisheries removing individuals from a population were subject to management. While we have tested the PBR approach with the US Seafood Import Rule specifically in mind, this article can be considered a case study for the broader management issue of spatial variation in management implementation. Shifts in the range and distribution of marine mammal populations, often bringing the animals into areas with different governance (e.g. across national borders, or from one fishing zone to another within a single country), are ongoing and likely to continue in the future. Efforts to manage the human activities that affect populations across their entire range would enhance recovery efforts.

Overall, the PBR approach is a robust way to facilitate the recovery of depleted marine mammal populations and to maintain them at MNPL, but it is important to remain cognizant of uncertainties that were not accounted for when the PBR approach was originally tested. More case-specific implications (e.g. population- or species-specific values for  $R_{MAX}$  and  $F_R$ ) are possible for those cases where data indicate greater levels of uncertainty or empirical evidence suggests lower (or higher) expected maximum rates of population growth.

### Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

### Data availability

All data are incorporated into the article and its online supplementary material.

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