RESEARCH ARTICLE

Can we manage marine mammal bycatch effectively in low-data environments?

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Abstract

1. Determining acceptable rates of human-caused mortality in low-data situations is a concern for many taxa world-wide. An established approach for determining acceptable levels of human-caused mortality of marine mammals and other species of conservation concern is the Potential Biological Removal (PBR) framework, but PBR requires near-unbiased estimates of absolute abundance, constraining its use in systems with limited data.

2. We develop three alternative methods for identifying acceptable levels of human-caused mortality for long-lived, slowly reproducing species, using indices of relative abundance combined with estimates of bycatch mortality in fisheries, and evaluate these methods using simulations similar to those used to develop PBR.

3. Across a variety of scenarios, the parameters of the three methods can be tuned to achieve conservation performance similar to that of PBR in scenarios that represent nearly ideal conditions. However, these methods produce lower and more variable bycatch mortality limits, depend upon reasonably accurate estimates of bycatch mortality and are more sensitive to uncertainties.

4. *Synthesis and applications*. Here we develop three alternative methods that expand the toolbox of approaches available for use in determining marine mammal conservation reference points for human-caused mortality when it is not possible to apply the more standard, data-hungry PBR approach. These approaches may be useful in supporting the establishment of new bycatch management programmes, or until estimates of absolute abundance become available.

1 | INTRODUCTION

Managing anthropogenic impacts on populations of conservation concern often involves identifying the causes, computing levels of impact (e.g. mortality) that populations can sustain and implementing regulations designed to achieve management goals. Although there are several sources of human-caused mortality of marine mammals, there is a general consensus among scientists and conservationists that the most prevalent source of such mortality is bycatch in fisheries (Read, 2005; Reeves et al., 2013). In addition, bycatch is the dominant driver of human-caused population declines and the primary barrier to recovery of depleted species and populations (Gales et al., 2003; Kovacs et al., 2012; Reeves et al., 2013).

The USA's Marine Mammal Protection Act (MMPA) provides the Potential Biological Removal (PBR) framework, which sets a level of human-caused mortality so that, with high probability, marine mammal populations will remain at, or recover to, their levels of maximal production. The PBR formula has been used to compute conservation reference points for human-caused mortality of marine mammals in many parts of the world (e.g. in the Baltic Sea, Berggren et al., 2002; New Zealand, Slooten et al., 2006; and Canada, Stenson et al., 2012) as well as for other animals subject to human-caused mortality (e.g. birds and bats; Diffendorfer et al., 2015).

To be consistent with fisheries terminology, herein we refer to PBR as a 'bycatch mortality limit'. However, in the USA's MMPA, PBR functions as a 'conservation reference point' or 'threshold' that triggers management actions if exceeded, and, unlike fisheries management, the goal of the MMPA is to drive mortality to be much lower than PBR. Calculating PBR typically requires an estimate of absolute abundance and its precision. Obtaining such estimates is not always possible, and it is particularly challenging in systems with resource and capacity limitations. Monitoring may more readily provide estimates of trends in relative abundance (i.e. abundance indices), which cannot be translated easily into absolute abundances (e.g. Taylor et al., 2007). Examples include: enumerating pinnipeds at only some rookeries or haul-out sites, surveying only a part of a population's range or conducting line-transect surveys of deep-diving cetaceans where a correction for availability bias is not available. Each of these examples would yield a negatively biased estimate of population size but could contribute to trend estimation.

Fisheries science has developed methods to support management of exploitation in the absence of absolute abundance estimates. This paper adapts three low-data fisheries methods to marine mammal populations experiencing bycatch mortality. Unlike PBR, these methods use estimates of removals (here, bycatch mortality). While data on marine mammal bycatch mortality are often sparse, imprecise and biased, these methods offer possible alternatives to PBR in situations where estimates of absolute abundance are unavailable or impractical to acquire. We use a simulation framework, following Wade (1998), parameterized to represent generic cetacean and pinniped populations to explore and compare the performances of the three alternatives and PBR.

2 | MATERIALS AND METHODS

2.1 | Testing framework

The testing framework involves projecting a simulated population forward when the limit on bycatch is set using one of the four methods, an approach known as management strategy evaluation (Bunnefeld et al., 2011; Punt et al., 2016). Simulated population dynamics are governed by the generalized logistic model used to develop PBR (Wade, 1998):

$$N_{y+1} = N_y + N_y R_{MAX} \left[1 - (N_y/K)^{\theta} \right] - B_y, \tag{1}$$

where N_y is the population size of the impacted species at the start of year y, K is the environmental carrying capacity, θ is the parameter that determines the proportion of K that maximizes production and B_y is the bycatch mortality during year y. Following Wade (1998), we used four base-case scenarios including two life-history types (Table 1a), and conducted eight sensitivity analyses (Table 1b). Abundance estimates were assumed to be proportional to true abundance and log-normally distributed, while bycatch mortality estimates were assumed to be unbiased and log-normally distributed with a pre-specified coefficient of variation (Appendix S1). The true human-caused mortality was assumed to be distributed about PBR according to a truncated normal distribution, reflecting the difficulty of implementing regulations for a bycatch mortality threshold.

2.2 | PBR method

PBR, typically calculated for a stock (population), is the product of three parameters: (a) a minimum estimate of abundance that 'provides reasonable assurance that the stock size is equal to or greater than the estimate'[1] (N_{MIN}); (b) one-half of the maximum intrinsic rate of population growth ($0.5R_{MAX}$); and (c) a recovery factor (F_R) between 0.1 and 1.0 (Wade, 1998):

$$PBR = N_{MIN} 0.5 R_{MAX} F_R. \tag{2}$$

Calculations of PBR herein use: N_{MIN} = the lower 20th percentile of the log-normal distribution of the most recent abundance estimate; default values for R_{MAX} (0.04 for cetaceans and 0.12 for pinnipeds),

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[1] Section 3(27) Marine Mammal Protection Act.

TABLE 1 Specifications of the trials to evaluate the efficacy of alternative methods to PBR. (a) Shows base-case values by life-history type. (b) Shows values for sensitivity analyses around key assumptions. (c) Shows values for sensitivity tests around survey frequency, and bycatch precision and bias. Dashes represent parameter values that are same as those for the base-case scenario. Parameter values that differ from the base-case scenario are denoted in bold. CV_N, CV_M and CV_C are the coefficients of variation about the estimates of abundance, actual bycatch mortality about the bycatch limit and the estimates of bycatch mortality, respectively. '~' denotes 'distributed as', and θ is the shape parameter for density dependence. A value of 1 under 'Abundance Bias' means the abundance estimates are unbiased, whereas a value of 2.00 means that the expected estimated value is twice the true abundance

(a) Base-case trial parameter values			
Case	Species	R_{MAX}	CV_N
A	Cetacean	0.04	0.2
B	Cetacean	0.04	0.8
C	Pinniped	0.12	0.2
D	Pinniped	0.12	0.8

(b) Sensitivity analyses (Wade, 1998); estimates of bycatch mortality are unbiased with a CV of 0.3

Trial	Description	R_{MAX}	CV_N	CV_M	Abundance bias	Initial depletion	Mortality ~ Normal (μ, σ^2)	Abundance survey interval (years)	θ
0A	Base case	Base	0.20	0.30	1	0.30	$\mu = $ PBR, $\sigma = CV_M \times $ PBR	4	1.0
0B		—	0.80	—	—	—	—	—	—
1A	Biased mortality	—	0.20	—	—	—	$\mu = 2 \times$ PBR	—	—
1B		—	0.80	—	—	—	$\mu = 2 \times$ PBR	—	—
2A	Biased abundance	—	0.20	—	**0.50**	—	—	—	—
2B		—	0.80	—	**2.00**	—	—	—	—
3A	Biased R_{MAX}	**0.5 × Base**	0.20	—	—	—	—	—	—
3B		**0.5 × Base**	0.80	—	—	—	—	—	—
4A	Bias in CV_N	—	**0.80**	—	—	—	—	—	—
4B		—	**1.60**	—	—	—	—	—	—
5A	Bias in CV_M	—	0.20	**1.20**	—	—	—	—	—
5B		—	0.80	**1.20**	—	—	—	—	—
6A	Survey every 8 years	—	0.20	—	—	—	—	**8**	—
6B		—	0.80	—	—	—	—	**8**	—
7A	MNPL = 0.45 × K	—	0.20	—	—	—	—	—	**0.53**
7B		—	0.80	—	—	—	—	—	**0.53**
8A	Biased mortality & MNPL = 0.70 × K	—	0.20	—	—	—	$\mu = 2 \times$ PBR	—	**5.04**
8B		—	0.80	—	—	—	$\mu = 2 \times$ PBR	—	**5.04**
9A	Population at MNPL	—	—	—	—	0.5	—	—	—
9B		—	—	—	—	0.5	—	—	—

(c) Sensitivity analyses (additional); Initial depletion = 0.3; bycatch mortality about the limit has a CV of 0.3; MNPL = 0.5

Trial	Description	R_{MAX}	CV_N	CV_M	Abundance bias	Bycatch bias	CV_C	Abundance survey interval (years)	First year with abundance data[a]	First year with bycatch mortality data[a]
0A	Base case	Base	0.20	0.30	1	1	0.3	4	20	20
0B		—	0.80	—	—	—	—	—		
10A	Biased abundance	—	0.20	—	**0.1–10**	—	—	—	—	—
10B		—	0.80	—	**0.1–10**	—	—	—	—	—
11A	Survey every year	—	0.20	—	—	—	—	**1**	—	—
11B		—	0.80	—	—	—	—	**1**	—	—

(Continues)

TABLE 1 (Continued)

| | | | | | | | | Abundance | First year with | First year |
Trial	Description	R_{MAX}	CV_N	CV_M	Abundance bias	Bycatch bias	CV_C	survey interval (years)	abundance data[a]	with bycatch mortality data[a]
(c) Sensitivity analyses (additional); Initial depletion = 0.3; bycatch mortality about the limit has a CV of 0.3; MNPL = 0.5										
12A	Survey every 2nd year	—	0.20	—	—	—	—	2	—	—
12B		—	0.80	—	—	—	—	2	—	—
12A	Biased estimates of bycatch mortality	—	0.20	—	—	**0.1–10**	—	—	—	—
12B		—	0.80	—	—	**0.1–10**	—	—	—	—
13A	CV of the estimates of bycatch mortality	—	**0.80**	—	—	—	**0.1–2**	—	—	—
13B		—	**1.60**	—	—	—	**0.1–2**	—	—	—
14A	Fewer abundance/ bycatch mortality estimates	—	0.20	—	—	—	—	—	10/5	10/5
14B		—	0.80	—	—	—	—	**—**	10/5	10/5

[a]Years before the first year the management system (i.e. a method for setting a bycatch mortality limit) is applied.

as applied in the United States; and values of F_R that are based on the conservation status of the stock (Wade & Angliss, 1997; Wade, 1998). The choice of the lower 20th percentile for N_{MIN} was motivated by US policy goals: (a) populations starting at the Maximum Net Productivity Level (MNPL, the analogue in the MMPA of the population size at maximum sustainable yield) have a 95% probability of being at that level after 20 years, and (b) populations starting at 0.3K recover to at least MNPL after 100 years (Wade, 1998).

2.3 | Alternative methods

The alternative methods for determining limits on bycatch mortality are based on time series of population abundance indices and removals due to bycatch mortality. These methods do not require removal estimates for all years, unlike some low data fisheries assessment methods (e.g. Cope, 2013), and, unlike some marine mammal management applications, where historical abundance is 'back-calculated' from a single abundance estimate and a near-complete history of bycatch mortality estimates (e.g. Smith, 1983). Table 2 lists alternative method parameters and values chosen for the simulations, and Appendix S2 provides the full mathematical specifications for the methods. The values for the parameters determining how many years of abundance index and bycatch mortality data are used [m, t and n below] were chosen based on performance for a set of base-case scenarios and these values were applied in several sensitivity analyses.

Other low data fisheries assessment methods that use length-frequency data or age-composition of catches to set catch limits (e.g. Wayte & Klaer, 2010) are not likely to be useful in management of marine mammal bycatch because the sample sizes for bycatch length-frequency or age-composition are rarely sufficient.

2.3.1 | The depletion-corrected average catch (DCAC) method

Depletion-corrected average catch (MacCall, 2009), which provides 'estimates of sustainable yield for low-data fisheries for long-lived species', is based on the potential-yield formula of Alverson and Pereyra (1969), while allowing for historical (and unsustainable) removals. The method quantifies uncertainty using a Monte Carlo procedure. For marine mammals, this could be any large-scale bycatch or mortality event that reduces the population to or below its MNPL. DCAC was originally developed to provide a 'once-off' value for sustainable yield, but is used here to determine bycatch mortality limits dynamically by updating the average catch and change in abundance over time. Given a time series of estimates of recent bycatch mortality and values for key parameters, DCAC computes the sustainable level of removals (total individuals removed), Y_{sust}, as:

$$Y_{sust} = \frac{\sum C}{n + \Delta / (0.5cM)}, \tag{3}$$

where $\sum C$ is the estimated bycatch mortality over the last n years of the available time series; Δ is the change in abundance based on a linear regression of the logarithms of observed abundance over the last m years (i.e. a potentially different time-series length than used for bycatch mortality), that is, $\log N_y^{obs} = a + sy$, where N_y^{obs} is the relative abundance index for year y; and c is the rate of population increase at MNPL divided by adult natural mortality M (i.e. $c = R_{MAX}/(2M)$ for a logistic production function). Equation 3 parameters, Δ, M and c, are assigned independent probability distributions (Table 2), which are sampled to construct a probability distribution for Y_{sust}. The bycatch threshold, set to Xth percentile of the distribution for Y_{sust} (X_{DCAC}^{th}), is selected to achieve a particular policy goal.

TABLE 2 Parameters of the alternative methods and their values for the simulations of this paper. All the methods require time series of abundance indices and bycatch mortality. There may be fewer than the ideal number of abundance indices and estimates of bycatch mortality when the methods are first applied and the specifications below cover these cases

Method/parameter	Specification
Depletion-corrected average catch (DCAC)	
n	20 years unless there are fewer estimates of bycatch mortality
M	20 years or chosen so there are at least recent five abundance indices (whichever is longer), or all years if there are fewer than five abundance indices
Δ	Log-normal with mean $1 - \exp(16 \times s)$ and standard error $16\exp(16\,s)\,\sigma_s$ where σ_s is the standard error of s. Δ is constrained to be <1
M	Uniform over [0.05 and 0.1/year] for the cetaceans (survival between 0.9 and 0.95) and [0.05 and 0.16/year] for the pinnipeds (survival between 0.84 and 0.95)
c	Log-normal with mean 1.0 and standard error of the logarithm of 0.2
X_{DCAC}	Tuning parameter selected to achieve a performance goal
Replacement yield (RY)	
t	20 years or chosen so that the period modelled has at least two abundance indices and two estimates of bycatch mortality
N_{initial}	Uniform over [$\overline{C}$, 2000], where $\overline{C}$ is the mean bycatch mortality for the 20 years prior to the first application of the method (or all estimates of bycatch mortality if there are fewer than 20)
P	Uniform over [0, $0.2\overline{C}$]
X_{RY}	Tuning parameter selected to achieve a performance goal
Slope	
n	20 years unless there are fewer estimates of bycatch mortality
m	20 years or chosen so there are at least recent five abundance indices (whichever is longer), or all years if there are fewer than five abundance indices.
x	Tuning parameter selected to achieve a performance goal

2.3.2 | The replacement yield (RY) method

The RY method uses a Bayesian estimation framework (Glazer & Butterworth, 2011) to fit a simple population dynamics model to abundance indices:

$$N_{y+1} = N_y + P - C_y, \tag{4}$$

where N_y is the number of animals at the start of year y (N_{initial}, Table 2, is the population size at the start of the simulation, set to be t years before application of the bycatch mortality threshold), P is the average annual net change in population size (i.e. births minus deaths) over the t-year period and C_y is the estimate of bycatch mortality for year y. P is assumed to be constant and

independent of population size because the change in production over t (here $t = 20$) years is likely small and would be hard to detect with few and imprecise data. The estimate of P is updated each time the RY method is applied, reflecting the best estimate of trend. Equation 4 is fitted to the abundance indices for the most recent t years, that is:

$$L = \prod_{y*} \left[\frac{1}{\sqrt{2\pi}\sigma} e^{-\frac{1}{2\sigma^2}\left(\log N_y^{\text{obs}} - \log(qN_y)\right)^2} \right], \tag{5}$$

where q is a constant of proportionality between the abundance indices and true abundances, σ is the standard error of log abundance indices and $y*$ denotes the set of years for which abundance indices are available during the most recent t years.

The Bayesian estimation framework is based on a sample-importance-resample algorithm (Rubin, 1987; Van Dijk et al., 1987), which generates parameter values from priors, computing the likelihood for each parameter vector and resamples from those parameter vectors, proportionally to the likelihood. To increase computational efficiency, the likelihood function is marginalized over q and σ, given priors $\log(q) \sim U[-\infty, \infty]$, and a prior proportional to $1/\sigma^2$, respectively (Walters & Ludwig, 1994). Application of the RY method leads to a posterior distribution for P, with the limit on bycatch mortality being set to the $X_{\text{RY}}^{\text{th}}$ percentile, where X_{RY}, the tuning parameter, is chosen to achieve a policy goal.

2.3.3 | The slope method

Several methods for determining catch limits have been developed that change fisheries removal limits proportionally to abundance (e.g. Magnusson & Stefanson, 1989). The Slope method version tested here sets a limit on human-caused mortality, C_{slope}, using the formula:

$$C_{\text{slope}} = \overline{C}\left(1 + m\,\widehat{\beta} + mx\,\sigma_{\widehat{\beta}}\right), \tag{6}$$

where $\overline{C}$ is the mean bycatch mortality for the n (=20) years before year y, the year for which a limit is needed, $\widehat{\beta}$ is the slope of a linear regression of observed abundance indices $\log N_y^{\text{obs}}$ on year y for the most recent m years, $\sigma_{\widehat{\beta}}$ is the standard error of $\widehat{\beta}$ and x is a tuning parameter that determines the extent to which the limit on bycatch mortality is reduced depending on the uncertainty of $\widehat{\beta}$, and is chosen to achieve a policy goal.

2.4 | Trials and performance metrics

Table 1a lists the specifications of the base-case trials for the productivity and abundance-index precision scenarios. The abundance estimates are unbiased and available every 4th year (but this is ignored in the alternative methods, which treat the abundance estimates as indices), the limit on bycatch mortality is updated

every 4th year, the true bycatch mortality is normally distributed about the threshold with a CV of 0.3, the estimates of bycatch mortality are obtained with a CV of 0.3, MNPL equals 0.5K (i.e. $\theta = 1$ in Equation 1), and the population is initially at 0.3K. Table 1b lists the original PBR sensitivity tests (Wade, 1998), as well as one in which the population is at MNPL when the management system is first applied.

Table 1c describes additional sensitivity analyses including biased bycatch mortality estimates and a broader range of bias in absolute abundance estimates, which only affects the performance of the PBR method. Also investigated were cases with more frequent abundance indices because it may be possible to obtain abundance indices more frequently than estimates of absolute abundance, as is true for grey whale *Eschrichtius robustus* calf counts (Perryman et al., 2011), California sea lion *Zalophus californianus* pup counts (Lowry et al., 2017) and vaquita *Phocoena sinus* abundance indices (Jaramillo-Legorreta et al., 2019). Finally, we analysed scenarios with fewer than the ideal number of abundance indices and estimates of bycatch mortality (Table 1c).

The performance metrics used to summarize simulation outcomes are the:

1. lower 5th percentile of the population size relative to K after 100 years;
2. probability that the population size exceeds MNPL after 100 years;
3. median, over all simulations, of the inter-annual variation in the limit on bycatch mortality, quantified using the average inter-survey variation AISV statistic (Brandon et al., 2017):

$$AISV = \sum_{ts=1}^{T} |HL_{ts+1} - HL_{ts}| \ / \ \sum_{ts=1}^{T} HL_{ts}, \qquad (7)$$

where HL_{ts} is the limit on bycatch mortality every 4th year (i.e. each time the bycatch mortality threshold is updated); and

4. median, over all simulations, of the total (over 100 years) of limits on bycatch mortality.

The first two were used by Wade (1998) and relate to achieving the recovery and maintenance goals of the MMPA. The third and fourth provide proxies for the impact of the management system on fisheries with marine mammal bycatch. All else being equal, higher, less variable bycatch mortality limits are preferred by fisheries over lower, more variable limits.

2.5 | Tuning alternative methods

The tuning parameters of the PBR formula are F_R and the percentile used to define N_{MIN}. The latter was set to achieve (a) a 0.95 probability of enabling a population to rebuild to its MNPL within 100 years (the 'recovery goal'), under ideal population dynamics and monitoring

conditions, when the population is initially at 0.3K; and (b) a 0.95 probability that a population initially at MNPL would be at or above that level in 20 years (Wade, 1998). The alternative methods have several potential tuning parameters (Table 2). The tuning parameters used here are the percentiles of the probability distributions for Y_{sust} for the DCAC method, P for the RY method and the parameter x in the Slope method.

Tuning involves two steps, corresponding to the way the PBR method is applied to populations that are above MNPL ($F_R = 1$) and those that are below MNPL but not considered highly depleted ($F_R = 0.5$). The tuning parameters are set for all base-case trials by first finding the values for the tuning parameters separately for each of two conservation performance metrics and for each abundance CV, and then selecting the most conservative parameter value in terms of risk. This process is conducted such that the two performance metrics are as high as those achieved by the PBR method for $F_R = 1$ and $F_R = 0.5$. As tuning is performed separately for the two life histories, there are four values for the tuning parameters for each of the alternative methods.

3 | RESULTS

Figure 1 compares outcomes among the four reference point-setting methods of a single trial for one cetacean population, an initial (year 0) abundance set at 0.3K, unbiased estimates of abundance with a CV of 0.2 provided every 4 years, bycatch mortality distributed about the removal limit with a CV of 0.3, unbiased estimates of bycatch mortality with a CV of 0.3 and MNPL set at 0.5K. The DCAC, RY and Slope methods (panels c–h) lead to wider ranges of outcomes than the PBR method (panels a–b). The DCAC and Slope methods also have a higher probability that population size will decline before recovering. All methods achieve recovery within 60 years. The range of limits on cetacean bycatch mortality is much wider for the RY method than for the other methods, in this example, with the PBR method leading to much less variation in bycatch limits than the other methods. The PBR method produces bycatch mortality limits that increase over time to an asymptote, whereas the DCAC method produces a declining trajectory of bycatch mortality limits and the RY and Slope methods lead to flat or slightly declining trajectories.

The three alternative methods lead to bycatch mortality limits that are equal to or, more frequently, less than those produced by the PBR method. This is most evident for the DCAC method for which the median of the total (over 100 years) bycatch mortality limits range between 23% and 57% of the median total bycatch mortality limits for the PBR method (Table S1).

For the base-case trials, all four methods lead to removal limits that achieve conservation goals in terms of the probability of recovery (≥0.95) and the lower 5th percentile of the population size relative to K after 100 years (>MNPL). Further, the PBR method performs adequately for all sensitivity tests, except when the actual R_{MAX} was lower than the default values. The performance of

FIGURE 1 Time trajectories of population size (relative to *K*) (left panels) and limits on bycatch mortality (right panels). Results are shown for the PBR method (a, b), and the three alternative methods (c–h). The blue lines are the medians, the light shading reflects the central 50% of the results, and the dark shading reflects the central 90% of the results. The red and green lines in the right panels are two, randomly selected, individual trajectories of bycatch limit. DCAC, depletion-corrected average catch; RY, replacement yield; Slope: the slope method
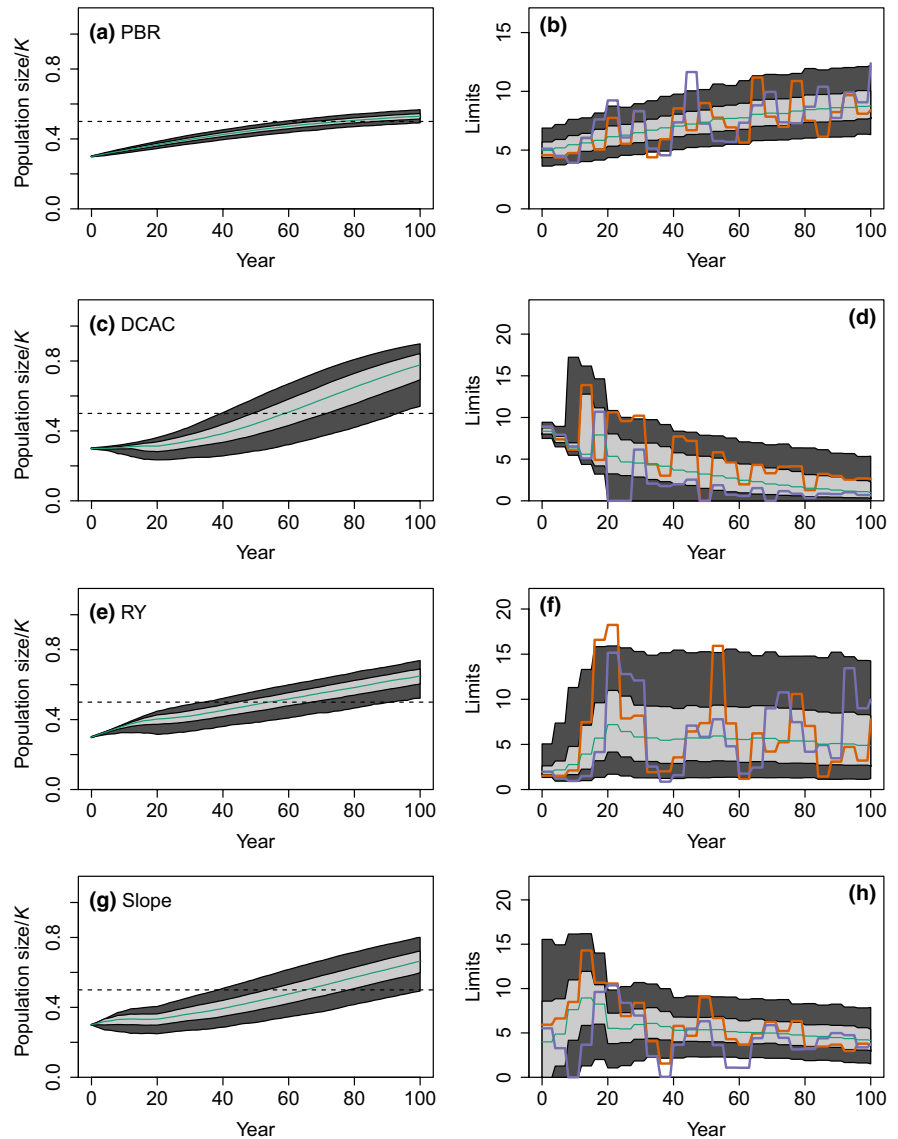
the alternative methods against conservation metrics (F_R = 0.5, Figure 2; F_R = 1, Figure S1) was sensitive to particular model parameters. In scenarios with unbiased bycatch mortality, a lower R_{MAX}, high CV about the mortality limit and less frequent abundance indices lead to lower probabilities of recovery for all three alternative methods, though those probabilities are at least 0.8 in most cases (Figure 2, top set of panels). In addition, the distribution of outcomes is wider when abundance indices are less frequent, with the consequence that several of the simulated pinniped populations collapse when management is based on the DCAC and Slope methods. Bycatch mortality that is biased, that is, twice the true mortality limit, leads to the poorest outcomes, particularly for pinnipeds (triangles in Figure 2). The results for the lower 5th percentile of the population size relative to *K* in 100 years (Figure 2, bottom set of panels) are similar to those for the probability of recovery, except that an underestimate of the abundance CV does not lead to adequate performance and only the Slope method performs inadequately for a survey frequency of 8 years.

Bias in bycatch mortality estimates has a major impact on the conservation-related performance metrics for the three alternative methods (Figures 2 and 3), especially for pinnipeds. When estimates of bycatch mortality are positively biased, probability of recovery and lower 5th percentile of population size drop precipitously for both taxa and that drop is amplified by uncertainty in abundance. Uncertainty in estimates of bycatch mortality, in contrast, impacts performance differently across life histories, with relatively little impact on cetaceans but a marked degradation in conservation performance in pinnipeds (Figure 4). Consequently, population collapse in pinnipeds occurs with bycatch mortality CVs above 0.3 for DCAC and above 0.8 for Slope and RY. Somewhat surprisingly, the total bycatch mortality limit and annual variation in bycatch mortality are not particularly sensitive to the CV of the estimates of bycatch mortality (Figure S2).

Survey frequency affects the performance of the alternative methods, but not that of the PBR method. The performances of the alternative methods generally deteriorate once survey frequency decreases to less than once every 4 years. However, there is little
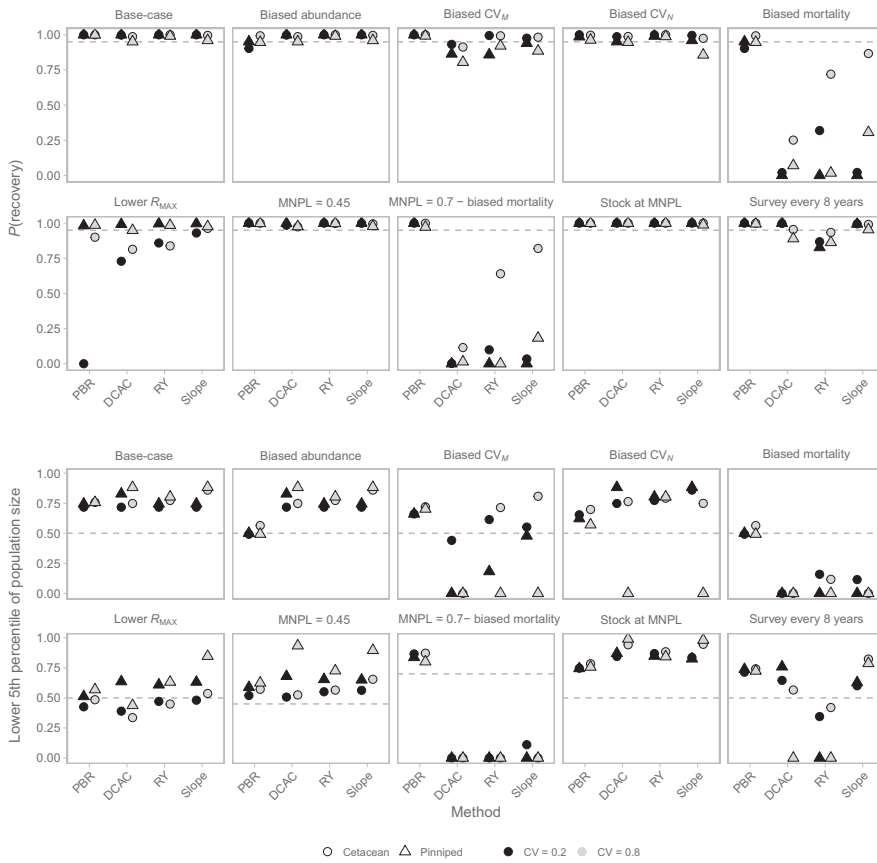
FIGURE 2 Values for the conservation-related performance metrics for the base trials and the nine sensitivity tests in Table 1b. The results in this figure pertain to the tunings that match $F_R = 0.5$ tuning of the PBR method
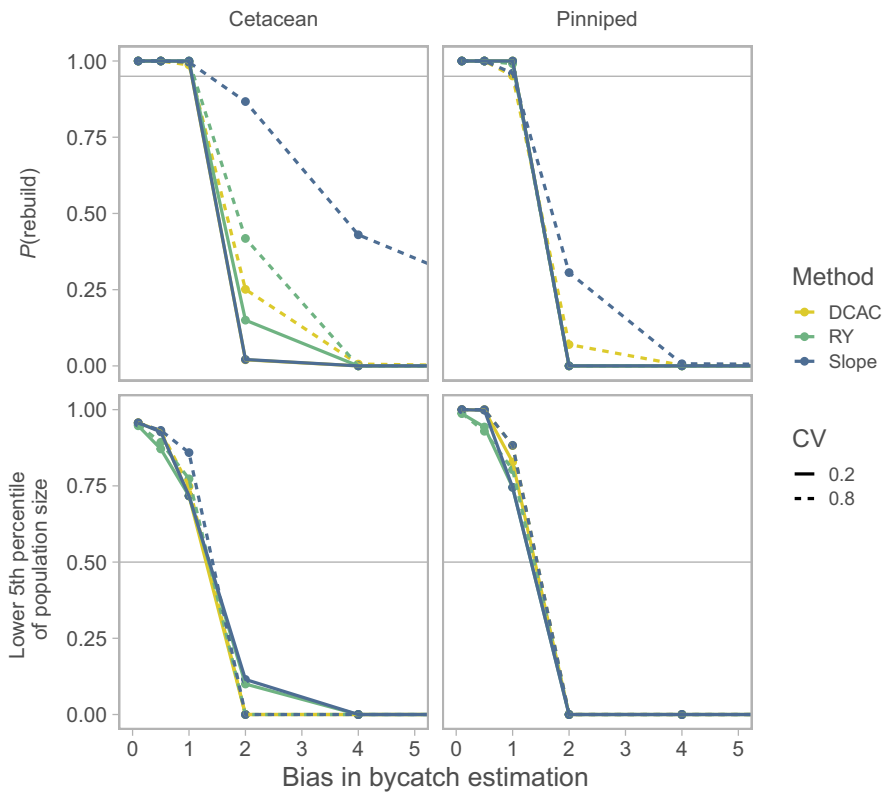

FIGURE 3 Performance of the alternative methods against conservation-related metrics with increasing bias in bycatch mortality estimation (ratio of expected to true value) for two levels for the CV of abundance indices

evidence of improved performance when there are fewer years between surveys. The conservation performance metrics are relatively constant for 1, 2, 3 and 4 years between surveys for the RY method

(green lines in Figure 5). In contrast, the DCAC and Slope methods perform worse when surveys are conducted more frequently than every 4 years, when the CV of abundance indices is 0.2, although

FIGURE 4 Performance of the alternative methods against conservation-related metrics with increasing CVs of bycatch mortality estimates, for two levels for the CV of abundance indices, and based on $F_R = 0.5$
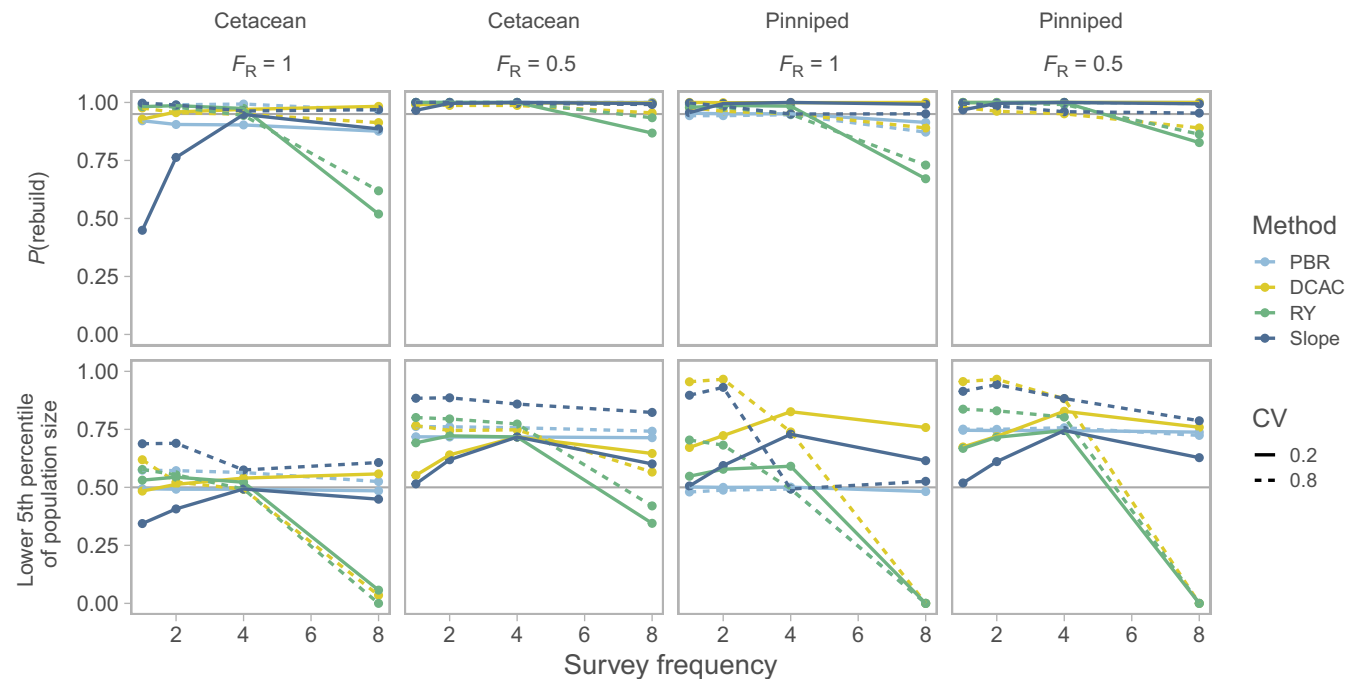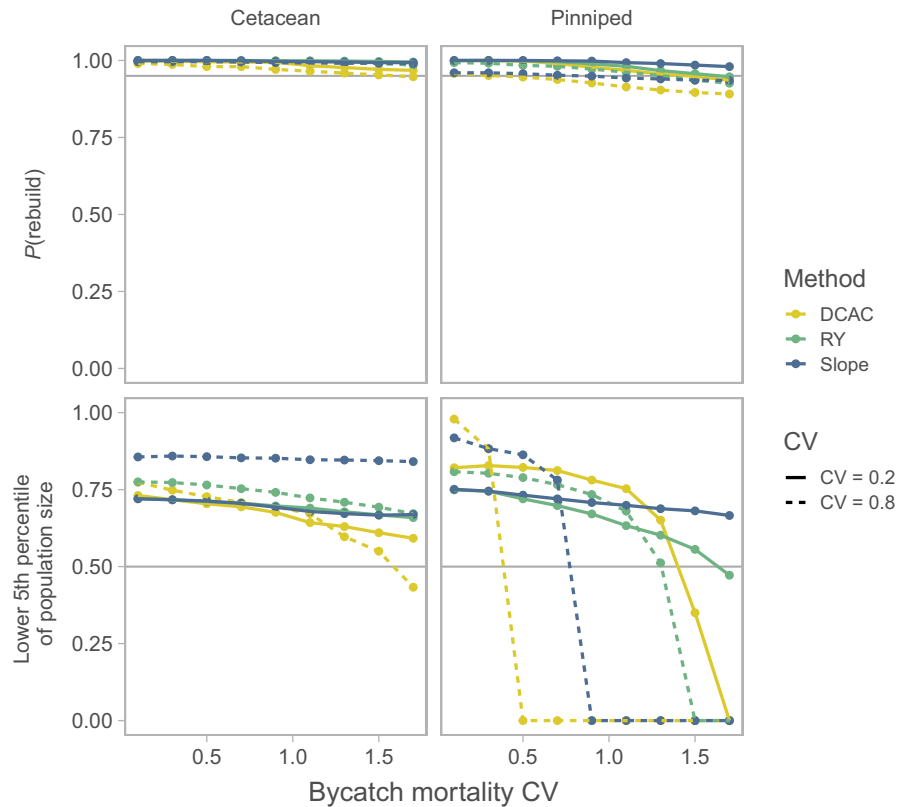

FIGURE 5 Performance of all methods against conservation-related metrics with increasing intervals between surveys, for tunings that match PBR tuning for $F_R = 1$ (columns 1 and 3) and $F_R = 0.5$ (columns 2 and 4), and for two levels for the CV of abundance indices

they achieve higher total bycatch mortality limits (Figure S3). The poor performance of the Slope method with increasing survey frequency relates to how the limit is adjusted given higher precision of the slope estimate associated with more frequent abundance indices (Figure S4).

The amount of initial data available before calculating limits impacts the methods differently. DCAC, but not RY or Slope, is robust to the number of abundance data points and bycatch mortality estimates prior to the first time the method is used to calculate limits, because it is more risk-averse in conservation terms in low-data

scenarios (Figures S5–S8). The RY method is most negatively impacted by a lack of initial data on abundance and bycatch mortality when the CV of the abundance indices is 0.2, particularly for pinnipeds. Adopting a tuning of the RY and Slope methods that matches the $F_R = 0.5$ variant improves conservation performance, but population collapse still occurs for pinnipeds.

4 | DISCUSSION

Our findings extend the set of methods available to support management efforts, particularly in low-data situations when estimation of absolute abundance is not possible but obtaining relative abundance indices is feasible. However, these alternative methods are in several ways less robust than PBR. Specifically:

- DCAC and Slope lead to more variable limits than PBR and have appreciably higher probabilities of decline in population size before population size increases, which would be a concern if the population was already depleted.
- Bycatch mortality limits are lower and more variable for the alternative methods, which would impose greater constraints on fisheries to achieve conservation objectives than would be necessary under a PBR framework.
- Bycatch mortality limits for DCAC decrease as population size increases, in contrast to the expectation under a policy that sets limits based on a constant rate of bycatch mortality (such as PBR). This arises because the average bycatch mortality is updated over time so a reduction in bycatch mortality (and hence average bycatch mortality) will tend to lead to lower limits in the future unless the population is increasing markedly. Although the limits from RY and Slope do not increase with increasing population size, they at least do not decrease. Implementation of the alternative methods would lead counter-intuitively to increasingly restrictive bycatch limits on fisheries when marine mammal population size is increasing.
- The three alternative methods depend on reliable estimates of bycatch mortality. Overestimation of bycatch mortality leads to the conclusion that the population is more productive than it actually is, and thereby to undesirable conservation outcomes. This arises because productivity is roughly scaled by removals and therefore overestimation of bycatch mortality leads to overestimation of production, and in turn to higher than warranted bycatch limits. Further, the effectiveness of the alternative methods depends upon reasonably accurate estimates of bycatch mortality, which can be a challenge in many cases.
- The alternative methods are much more sensitive to survey frequency than is PBR, particularly for pinnipeds. In many systems, abundance surveys occur but at low frequencies (i.e. intervals of more than 4 years). Investing in more frequent monitoring, therefore, can bolster the utility of these alternative approaches.

Figure 6 summarizes how managers should select a method for setting limits. The results highlight the considerable value of obtaining
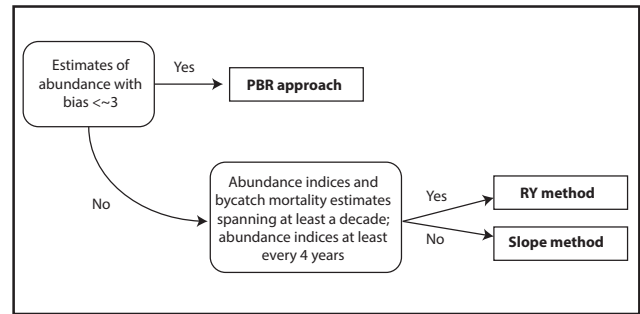

FIGURE 6 Decision tree for determining which method to use in determining bycatch mortality limits based on available information. The depletion-corrected average catch method is not recommended because it requires the same data as the Slope method, but performs more poorly. Bias is defined as the ratio of the expected estimated abundance to the true abundance

estimates of absolute abundance when possible, and hence the preferability of using the PBR method. However, if only abundance indices can be obtained, the RY method should be used unless surveys are conducted infrequently (e.g. every 8 or more years, compared to every 4 years), or relative abundance data and estimates of bycatch mortality do not span at least 10 years, in which case the Slope method should be applied. However, the tuning parameter of the Slope method would need to be adjusted to reflect survey frequency, because performance of this method depends on survey frequency (Figure 5; Figure S4). The DCAC method is not advocated in any scenario.

The poorer performance of the alternatives relative to PBR is not surprising because the availability of absolute abundance estimates (even with poor precision) is known to improve the performance of management strategies. This is one reason that estimates of absolute abundance rather than abundance indices served as the basis for the management strategies for commercial and aboriginal subsistence whaling developed by the Scientific Committee of the International Whaling Commission, IWC (Kirkwood, 1992).

The alternative methods are more sensitive than PBR to the values of the parameters in the simulation model, and this suggests that it would be useful to develop case-specific simulations and algorithms for setting limits, an approach taken by the IWC for aboriginal subsistence whaling. Such case-specific simulations could be based on more sophisticated operating models, including those with age, sex and spatial structure (e.g. IWC, 2014). Another direction for future work would be to test a method that uses absolute abundance estimates and relative abundance indices. Such a test could be based on the RY method and consider estimating the relationship between production and abundance given additional data.

Results are shown for two tunings of each alternative method. However, other tunings are possible, for example, based on higher or lower probabilities of rebuilding to MNPL. In addition, different values for t, n and m (Table 2) could be considered, especially if the frequency and precision of the abundance indices differed from the base-case values examined here.

Historically, estimates of bycatch mortality have often been based on observer programs, but alternative approaches such

as the application of reverse drift models to strandings data (e.g. Peltier et al., 2016, 2020), and use of remote electronic monitoring (e.g. Kindt-Larsen et al., 2016) may provide alternatives to observer data.

Setting limits on removals with a method that uses estimates of absolute abundance is ideal when the marine mammal bycatch is known or likely to be unsustainable, but this is not always feasible. If absolute abundance estimates are not available, a reasonable alternative approach is needed to determine reference points for marine mammal bycatch mortality, while the resources and capacity are developed to produce them. The present exploration of alternative methods also provides guidance for data collection when management can only be based on removals and relative abundance. Specifically, investment in regular, precise estimation of bycatch mortality and surveys of relative abundance at least as often as every 4 years are necessary, and should be the minimal monitoring goal when PBR-based management is untenable.

ACKNOWLEDGEMENTS

AUTHORS' CONTRIBUTIONS

A.E.P. identified the research question, developed the methods, coded the models and led the writing; J.M., M.S., T.B.F. and P.R.W. identified the scenarios. All the authors contributed to interpretation of results, writing and editing, and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The code used to conduct the analyses is available via the https://github.com/OceanModelingForum/punt-et-al-2020-japplecol (Punt et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Punt AE, Siple MC, Francis TB, et al. Can we manage marine mammal bycatch effectively in low-data environments? *J Appl Ecol*. 2020;00:1–12. https://doi.org/10.1111/1365-2664.13816