Ministry for Primary Industries
Manatū Ahu Matua

Application of Potential Biological Removal methods to seabird populations

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EXECUTIVE SUMMARY

The Potential Biological Removal (PBR) approach was developed in response to the United States Marine Mammal Protection Act, to identify populations experiencing human-caused mortality at levels that could result in population depletion. The PBR is calculated from the maximum population growth rate (r_{max}) and a lower estimate of the population size (N_{min}), as $PBR = \frac{1}{2} r_{max} N_{min} f$, where f (typically between 0.1 and 0.5) is a "recovery factor" that may be set lower to allow a population to recover faster, or to provide additional protection to the population. If the human-caused mortalities are less than the PBR, then a depleted population will be able to recover so that, given sufficient time, it has a 95% probability of being over half the carrying capacity.

When assessing the potential impact of human-caused mortalities on seabird populations, the PBR has been used as a guide to the productivity of the seabird populations. Applying the PBR to seabirds is difficult as neither the maximum growth rate nor the total population size can be directly measured. Instead, approximations must be used that allow estimation of these parameters from readily available data.

In this report, we used simulations of seabird demography to assess the accuracy of these approximations. This approach involved three main steps. First, we simulated the population dynamics for 12 types of seabirds, representing a range of species breeding in New Zealand. For each species type, we estimated the maximum human-caused mortality rate that the populations could incur, while still being able to recover to above half the carrying capacity, with 95% probability, in the presence of both environmental and demographic stochasticity. Second, we generated a PBR estimate using an approximate maximum growth rate and population size. The PBR estimate included a parameter ρ, calibrated so that the base PBR (PBR_b; evaluated with $f = 1$ and with the total population, N, rather than the conservative estimate, N_{min}) had only a 5%-probability of exceeding the maximum human-caused mortality. Finally, we explored the effect of errors or bias in the demographic parameters used for the calculation of the PBR, to provide guidance in setting the value of the recovery factor, f.

The analysis showed that the approximate base PBR derived from demographic parameter estimates tended to overestimate the maximum human-caused mortality. Inclusion of a calibration factor, ρ, was required to adjust the PBR approximations to meet the management criterion; ρ varied between 0.17 and 0.61, depending on the species types. In general, the calibration factor was smaller for species with slower growth rates, such as albatrosses, and higher for species with higher growth rates, such as shags and penguins. Previous estimates of the PBR for seabird populations that did not include this calibration factor are likely to have overestimated the human-caused mortalities that the populations could incur.

The choice of f values will depend on what errors in the underlying parameters are considered plausible, and on requirements for the recovery time of depleted populations. In this report, some exploration of the consequences of incorrect estimates of the parameters is given, but an explicit recommendation for the choice of f values is not made.

With the inclusion of the additional calibration factor, ρ, the method for calculating the PBR described here provides a simple way for determining whether fishing-related mortalities are sufficiently low that seabird populations are able to recover to and/or remain at above half the carrying capacity in the long term.

1. INTRODUCTION

Seabirds are killed during fishing in New Zealand waters (Bartle 1991, Baird & Smith 2008, Waugh et al. 2008, Abraham & Thompson 2011a, Ramm 2012). Recent estimates are that around 5000 seabirds are killed annually in New Zealand trawl and longline fisheries, without including cryptic mortalities that would not be recorded by fisheries observers (Abraham et al. 2013). Seabirds have also been reported caught in recreational, commercial set-net, and other fisheries (e.g., Abraham et al. 2010, Abraham & Thompson 2011b, Ramm 2012). Several risk assessments have been carried out in recent years, on behalf of Ministry for Primary Industries and Department of Conservation, to assess the potential effect of fishing-related fatalities on New Zealand seabird populations. These risk assessments include approaches that use qualitative scoring to assess the population impacts (Rowe 2010), known as level-1 assessments (Hobday et al. 2011), and semi-quantitative or level-2 assessments (Sharp et al. 2011, Waugh et al. 2009, Richard et al. 2011). The level-2 risk assessments use both an estimate of the number of fishing-related fatalities, and a quantitative assessment of the likely impact of these fatalities on the respective seabird populations.

Recent semi-quantitative risk assessments have used the Potential Biological Removal (PBR) method to determine a threshold of the number of fatalities that a population may incur. The PBR was developed under the United States Marine Mammal Protection Act for managing the impacts of fishing on marine mammal populations (Wade 1998). It may be calculated in the absence of detailed demographic information, from the maximum population growth rate ($r_{\max}$), a conservative estimate of the total population size ($N_{\min}$), and a recovery factor (f):

$$\text{PBR} = \frac{1}{2}r_{\max}N_{\min}f \tag{1}$$

The PBR allows for uncertainty in the estimation of the total population size, N, by including a conservative estimate of that parameter, $N_{\min}$. In the original approach by Wade (1998), a recovery factor of $f = 0.5$ was included to allow for potential errors in the estimation of the growth rate and population size parameters. Restricting fishing-related mortalities further, by adopting a recovery factor less than 0.5, allowed for other management criteria to be met, such as allowing depleted populations to recover more rapidly (Wade 1998, Taylor et al. 2000). In recent seabird risk assessments, different values between 0.1 and 0.5 were chosen for the recovery factor, depending on the conservation status of the seabird population concerned (Waugh et al. 2009, Richard et al. 2011, Dillingham & Fletcher 2011).

To apply the PBR approach to seabirds, a management criterion for seabird populations is required that allows managers to determine whether human-caused mortalities will have an unacceptable impact on the seabird population. An example of a criterion is the MNPL (maximum net-productivity level) goal used for developing the PBR by Wade (1998), which required that in the presence of ongoing human-caused fatalities, populations initially at 30% of the carrying capacity recover to at least the MNPL after 100 years. For populations with a linear relationship between density and growth rate (such as populations following logistic growth), the MNPL occurs at half the carrying capacity. Following discussion with the Ministry for Primary Industries, a closely related criterion was adopted as the primary measure to be used for seabird populations in New Zealand waters. It required that populations would have a 95% probability of being above half the carrying capacity after 200 years, in the presence of ongoing human-caused mortalities, and environmental and demographic stochasticity (Figure 1). This criterion was considered to be consistent with the current approach to managing fishery impacts on seabird populations. In a simulation context, the management criterion was defined as the requirement that:

- based on initial populations that are uniformly drawn from between 5% and 100% of the carrying capacity, then

- after 200 years, 95% of simulated populations will be above half the carrying capacity.

The maximum mortality rate (MMR) was then defined as the maximum proportion of the population that may be killed annually through human causes, while still meeting the management criterion. The maximum mortality (MM) from human causes that can occur is $MM = N\,MMR$, where N is the total population. The PBR should then satisfy the following constraint:

$$PBR_b \leq MM, \tag{2}$$

where the base PBR, PBR_b, is defined as the PBR with $f = 1$ and with the total population N, rather than a minimum value ($PBR_b = \frac{1}{2}r_{\max}N$). In Equation 2, the base PBR is expected to be as high as possible, while still satisfying the inequality. Strict equality is not possible in general, as the maximum human-caused mortality will not have the simple algebraic form of PBR_b. Even without the recovery factor, or without taking a minimum estimate for the population size, the human-caused mortalities should be sufficiently low that the seabird populations are able to be maintained above half the carrying capacity, provided that the PBR is correctly estimated.

The calculation of the base PBR (Equation 1) requires an estimate of the total population size and maximum growth rate. The total population size is generally unknown for seabird species. Typically, the number of annual breeding pairs is estimated from surveys of colonies, and the total population size must be derived from the number of breeding pairs. Approaches for calculating the total population size have included the use of "rule-of-thumb" multipliers (e.g., Waugh et al. 2009), allometric relationships (Dillingham & Fletcher 2011), and simple models assuming constant survival among age classes (e.g., Gilbert 2009, Richard et al. 2011). Gilbert (2009) calculated an approximation to the total population, N^G, from the number of breeding pairs, age at first reproduction, proportion of adults breeding in a year, and adult survival. This approximation may be used to estimate the PBR.

The maximum growth rate, $r_{\max}$ is also unknown for most seabirds. Niel & Lebreton (2005) developed a method to calculate an approximation, $r_{\max}^{NL}$, to the maximum growth-rate from adult survival and age at first reproduction only, based on allometry and life-history theory. An approximation to the base PBR (denoted PBR_b^*) may then be calculated as:

$$PBR_b^* = \frac{1}{2}r_{\max}^{NL}N^G. \tag{3}$$

The use of the approximations allows for a tractable calculation of the PBR (through Equation 3), and this method was used previously to assess the risk of fishing to seabirds (Richard et al. 2011). Here, we used a simulation approach to calibrate the approximations in Equation 3, and to adjust the resulting PBR to meet the management criterion above. Population simulations were used to generate populations that had a known maximum growth rate $r_{\max}$ and total population size N. The maximum mortalities were then calculated from the simulated populations, and we defined a calibration factor ρ, so that

$$\rho PBR_b^* \leq MM, \tag{4}$$

where the inequality was satisfied for 95% of the simulated populations. The simulations were made for a range of seabird types, representing different life-histories. In addition to calculating the calibration factor ρ, we carried out a sensitivity analysis that may be used to assist in choosing suitable values for f.

The inclusion of the calibration factor, so that the calculated PBR is related to an explicit management criterion, improves on the risk assessment method used by Richard et al. (2011). The calibration factor compensates for possible errors in the approximations used to calculate the maximum growth rate and the total population size. It also allows the PBR to satisfy the management criterion in the presence of
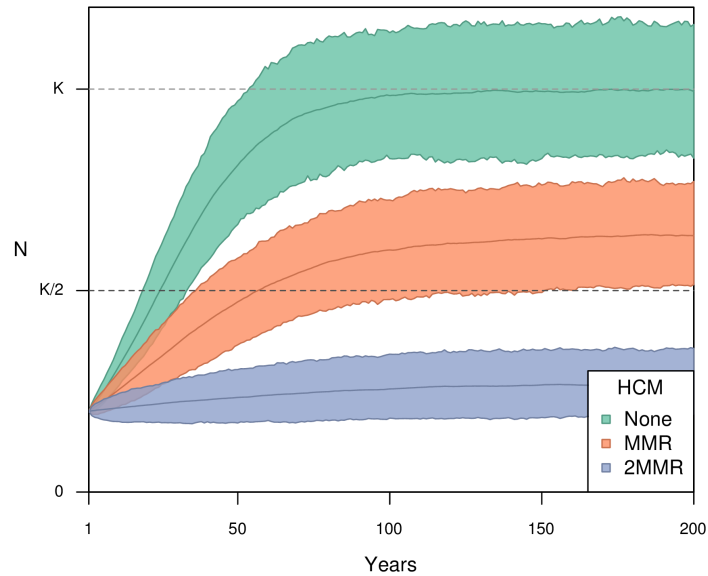
Figure 1: Illustration of the management criterion, showing repeated 200-year simulations of a seabird population. The green shading marks the 90% confidence interval of a set of populations with no human-caused mortality (HCM), with orange shading marking the confidence interval of a set of populations with mortality at the maximum mortality rate (MMR). With mortality at the MMR, 95% of the population trajectories are above half the carrying capacity ($K/2$) after 200 years. These populations just meet the management criterion. The blue shading indicates the envelope of trajectories of populations with mortalities at twice the MMR.

some environmental variability.

2. METHODS

2.1 Demographic model

Simulations were used to assess the impact of a range of human-caused mortality rates on a seabird population with given demographic parameters. The simulations used a simple population model. This model is age-structured, with a pre-breeding census (Caswell 2001). The model had $A - 1$ classes for immatures (one year old or over), where A was the age at first reproduction, and two classes for adult males and females (Figure 2). All birds of age A were assumed to become adult with the potential to breed. Birds less than one year old (chicks) were assumed to be born just after an annual census, and were considered to be one-year-old immatures at the next census (Caswell 2001). Males and females were not differentiated until they were adults, at which stage sexes may behave differently, allowing for the possibility of class-based mortality biases, which have been detected in some species caught in fisheries (Murray et al. 1993, Croxall et al. 1990, Nel et al. 2002).

For a given year, the annual cycle was modelled as follows:

1. *Pair formation*. The number of potential pairs was determined by the minimum number of adult males or females. Each potential pair breeds that year with a mean probability P_B, constant among years.

2. *Reproduction*. Each breeding pair lays E eggs (where E is a fixed value for each species), and each egg hatches into a chick surviving until the following year with a mean probability S_C.
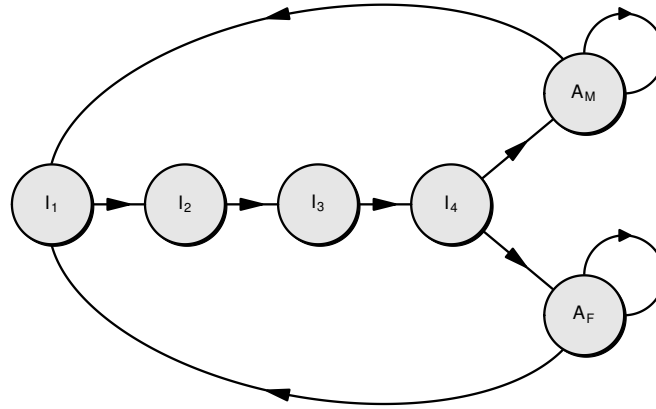
Figure 2: Diagram of the population model used to predict the persistence of a seabird species, when the age at first reproduction (A) is five years. Each circle represents an age class, I_a for immatures of age a, and A_M and A_F for adult males and females, respectively. The arrows represent the modelled transitions from year to year between classes.

3. *Survival.* A proportion of immatures, adult males, and adult females dies from natural causes, with respective probabilities $1 - S_I$, $1 - S_M$, and $1 - S_F$.

4. *Human-caused mortality.* A proportion H of the total population, constant among years, dies from human-related factors. For a total human-caused mortality rate H, the human-caused mortality rate H_i of class i is a function of the proportion of the class in the population, π_i, and of the class-specific vulnerability v_i, allowing a differential mortality between age classes or sexes:

$$H_i = H \frac{v_i}{\sum_{j \in \{I,M,F\}} v_j \pi_j},$$ (5)

For example, if $v_I = 1$, $v_M = 1$, and $v_F = 2$, adult females are twice as likely to be killed from anthropogenic factors than adult males and immatures. But if $v_I = 1$, $v_M = 2$, and $v_F = 2$, immatures are half as likely to be killed than adults.

5. *Transitions.* Immatures move to the next age class, surviving chicks become immatures of age 1, and all immatures of age at first reproduction $A - 1$ become adults.

The base model, i.e., without density dependence, stochasticity, or distributions for the parameters, and with equal numbers of adult males and females, can be represented by the following transition (Lefkovitch) matrix in the case of an age at first reproduction of $A = 5$ years:

$$M = \begin{bmatrix} 0 & 0 & 0 & 0 & \frac{1}{2}EP_BS_C & \frac{1}{2}EP_BS_C \\ S_I(1-H_I) & 0 & 0 & 0 & 0 & 0 \\ 0 & S_I(1-H_I) & 0 & 0 & 0 & 0 \\ 0 & 0 & S_I(1-H_I) & 0 & 0 & 0 \\ 0 & 0 & 0 & \frac{1}{2}S_I(1-H_I) & S_M(1-H_M) & 0 \\ 0 & 0 & 0 & \frac{1}{2}S_I(1-H_I) & 0 & S_F(1-H_F) \end{bmatrix}, \quad (6)$$

where E is the clutch size, P_B the adult breeding probability, S_C the annual natural survival rate of chicks

(from the laying of the egg to 1 year old), S_I the annual natural survival rate of immatures (from 1 year-old to $A - 1$), S_M and S_F the annual natural survival rate of adult males and females, respectively (A years old and more), and H_i the human-caused mortality rate of class i.

With the transition matrix, M, in the absence of density dependence and stochasticity, the population size for all classes at year $t + 1$ can be calculated from the previous year t using the following matrix multiplication:

$$
\begin{bmatrix} I_1 \\ I_2 \\ \cdots \\ I_{A-1} \\ A_M \\ A_F \end{bmatrix}_{t+1} = M \times \begin{bmatrix} I_1 \\ I_2 \\ \cdots \\ I_{A-1} \\ A_M \\ A_F \end{bmatrix}_t ,
$$

where I_i is the number of immatures of age i, and A_M and A_F are the number of adult males and the number of adult females, respectively. This matrix model was used for initialising the populations.

2.2 Demographic and environmental stochasticity

It is well recognised that random variations in growth rate can affect population trajectories and generate a risk of extinction even when their intrinsic growth rate is positive (Tuljapurkar & Orzack 1980). Random variations can occur from the probabilistic realisation of discrete events such as births and deaths. This variability, called demographic stochasticity, is generally only important when population sizes are small. It was included in the model here, by drawing the number of survivors, breeding pairs, and eggs laid from a binomial distribution at each step.

Random variations can also occur because of the natural variability in the physical environment, such as temperature and rainfall (or stochastic events such as storms), or in the biotic environment, such as food availability. Such environmental stochasticity was included by adding some year-to-year random variation to the survival rate of chicks, immatures, and adults, assuming a beta distribution of these rates (Kendall 1998, Samaranayaka & Fletcher 2010). The same annual variation was applied to all three age classes, by applying the inverse function of the beta distribution to a random variable uniformly distributed between 0 and 1, equal among classes, and by specifying the two shape parameters (α and β), so that the mean matched the mean survival rate μ_i of each class i, and the standard deviation matched the level of environmental stochasticity (σ_S; see Section 2.4), using the formulae (Samaranayaka & Fletcher 2010):

$$
\alpha = \mu \left(\frac{\mu(1 - \mu)}{\sigma_S^2} - 1 \right), \qquad \beta = \frac{(1 - \mu)\alpha}{\mu}.
$$

Environmental variation was measured through the coefficient of variation (c.v.) of the population size, the specific form of how it was parametrised within the model was not expected to be important.

2.3 Density dependence

Density dependence was applied to chick and adult survival, as well as to the breeding probability of adults, to represent competition for breeding space and mates, and aggression towards chicks in crowded environments. In general, the mechanism and functional form of density dependence are not known.

However, we used the following Beverton-Holt function for this purpose (Caswell 2001):

$$\phi = \frac{\phi_0}{1 + (C_{DD}N)^\theta},$$ (7)

where ϕ is the vital rate under density dependence, ϕ_0 the vital rate without density dependence, C_{DD} the strength of density dependence, and N the total population size. The dimensionless parameter θ is the strength of the density dependence. A value of 1 gives a linear relationship between population size and growth rate, corresponding with logistic growth. Values greater than 1 give a convex relationship, with growth being less affected by density dependence at low population sizes (Figure 3). As the non-linearity increases, the relative population size that yields maximum productivity (MNPL) also increases. The parameter θ was fixed to 1 throughout the study, and some sensitivity analysis of the PBR to non-linear convex density relationships ($\theta > 1$) was carried out.
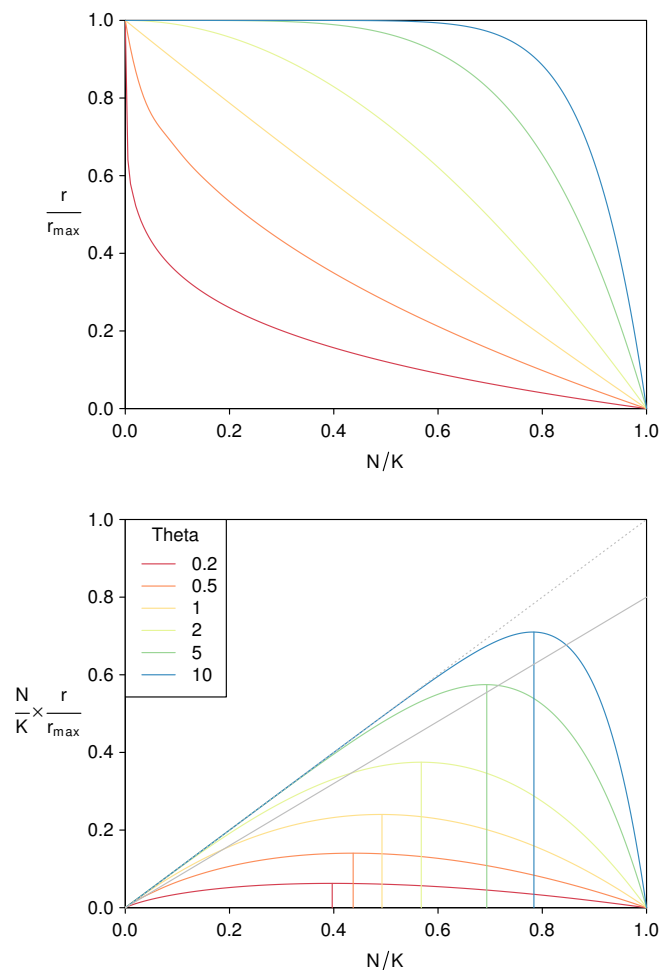
Figure 3: Density dependence of the growth rate from the Beverton-Holt function, for a range of the density parameters, theta (θ). The top graph gives the growth rate, relative to the maximum growth rate, as a function of the population size, relative to the carrying capacity. The lower graph gives the net productivity (the product of the population size and the growth rate, relative to the product of the carrying capacity and the maximum growth rate).

The carrying capacity of the environment was not explicitly included in the model, but was determined by C_{DD}, and the carrying capacity was calculated for each sample of parameter values by simulating 1000 trajectories for 200 years without human-caused mortality, but with stochasticity included in the model. The carrying capacity was defined as the mean population at 200 years from the 1000 simulations.

Trajectories were initialised by randomly sampling from a uniform distribution between 5% and 100% of the carrying capacity.

2.4 Initial conditions

Simulations were carried out for twelve seabird types, representing a range of life-history characteristics (Table 1). Values of vital rates were obtained from the literature (see Richard et al. 2011), including survival rates for chicks, immatures, and adults, the probability of breeding, clutch size, and age at first reproduction.

For each type, an underlying maximum growth rate (λ_{max}) was set, which represents the growth of the population in the absence of human-caused mortality or of any density-dependent effects. The maximum growth rate was chosen by initial exploration of the population dynamics of each species type, and by reference to the literature where previous estimates were available (e.g., Dillingham & Fletcher 2011). The parameters for each of the species types provide a set of self-consistent estimates of demographic parameters and associated maximal growth rates, covering a range of λ_{max} values from 1.04 for Antipodean albatross to 1.22 for Caspian tern (Table 1).

Table 1: Demographic parameters for each type of seabird used to create samples for simulations of population dynamics. A: age at first reproduction; E: clutch size; $S_{C,I,A}$: annual survival rate of chicks, immatures, and adults, respectively; P_B: probability of breeding for adults; λ_{max}: maximum population growth rate.

Species type	A	E	S_C	S_I	$S_{A_{min}}$	$S_{A_{max}}$	$P_{B_{min}}$	$P_{B_{max}}$	λ_{max}
Antipodean albatross	11	1	0.74	0.90	0.96	0.98	0.55	0.75	1.04
Grey-headed albatross	10	1	0.70	0.85	0.95	0.97	0.55	0.75	1.04
Giant petrel	7	1	0.70	0.80	0.92	0.94	0.80	0.90	1.05
Black petrel	5	1	0.46	0.79	0.90	0.95	0.73	0.90	1.06
Flesh-footed shearwater	6	1	0.77	0.85	0.92	0.94	0.70	0.95	1.07
Fairy prion	4	1	0.70	0.80	0.84	0.92	0.80	0.95	1.08
Common diving petrel	2	1	0.65	0.70	0.83	0.90	0.80	0.95	1.08
Storm petrel	3	1	0.70	0.80	0.90	0.92	0.80	0.95	1.09
Shag	3	2	0.70	0.80	0.88	0.90	0.75	0.95	1.19
Erect-crested penguin	3	2	0.50	0.75	0.84	0.90	0.70	0.90	1.16
Yellow-eyed penguin	3	2	0.51	0.75	0.87	0.92	0.60	0.90	1.16
Caspian tern	3	2	0.70	0.80	0.89	0.91	0.80	0.95	1.22

Simulations were carried out for each of the species types included in Table 1. For the simulations, sets of values for the demographic parameters, called parameter samples, were initially drawn randomly, according to the following rules: the age at first reproduction and the clutch size were assumed to be constant, and fixed to the field estimates (A and E, respectively). Survival rates for chicks and immatures were drawn from a uniform distribution between the field estimates (S_C and S_I, respectively) and 1, and between the field estimate ($S_{A_{min}}$) and a maximum value ($S_{A_{max}}$) for adults. Samples of the survival rates were only accepted if the adult survival was greater than that of both chicks and immatures. The probability of breeding for adults was drawn from a uniform distribution between $P_{B_{min}}$ and $P_{B_{max}}$.

The space of parameter values was then constrained so that the maximum population growth rate of each sample (λ_{max}) matched the values in Table 1. Many samples of the demographic parameters generated population trajectories with biologically unrealistic growth rates. Given a sample of demographic parameters, the population growth rate λ can be calculated as the dominant eigenvalue of the transition matrix (Caswell 2001). Nevertheless, in a stochastic environment, a population might decline even

though the deterministic growth rate is positive, because the geometric mean is always lower than the arithmetic one, and population growth involves a series of both additive and multiplicative processes. For this reason, instead of calculating the deterministic growth rate λ, we calculated the stochastic growth rate λ_S for each sample, by taking the geometric mean of the annual growth rates ($\lambda_t = N_{t+1}/N_t$) of 100 trajectories over 100 years using the stochastic model, but without density dependence. A Monte-Carlo process was then used to select parameter samples so that λ_S followed a log-normal distribution, with the 95% confidence interval from $\lambda_{max} - 0.01$ to $\lambda_{max} + 0.01$. The width of this distribution was chosen to be small relative to the range of λ_{max} values across all the species types. This process was achieved for each species type by accepting sets of values based on a probability calculated from the normalised ratio of the probability density of the desired log-normal distribution to the empirical distribution of stochastic growth rates obtained by simulations.

The maximum level of environmental stochasticity was chosen so that the coefficient of variation of the population size at $K/2$ was 0.2. This level of environmental stochasticity was reached with a standard deviation of survival rates between 0.05 for albatrosses and 0.10 for terns. The range of environmental stochasticity considered here covered the range of values reported in long-term studies in the literature (e.g., Lescroël et al. 2009, Bell et al. 2011). Monte-Carlo resampling was used to ensure that the final simulations had the required distribution of stochasticity. After this sampling, 5000 samples were accepted for each species type (Table 2).

Table 2: Distributions of demographic parameters for each type of seabird that were used for the simulations. The parameters were constrained to have the specified maximum growth-rate distribution and environmental stochasticity. Presented are mean values and 95% confidence intervals of λ_S, stochastic growth rate; S_C, S_I, S_A, annual survival rate of chicks, immatures, and adults, respectively; P_B, probability of breeding for adults; and σ_S, standard deviation in survival rates (see values of age at first reproduction, A, and clutch size, E, in Table 1.)

	λ_S		S_C		S_I		S_A		P_B		σ_S	
	Mean	95% c.i.	Mean	95% c.i.	Mean	95% c.i.	Mean	95% c.i.	Mean	95% c.i.	Mean	95% c.i.
Antipodean albatross	1.04	1.03–1.05	0.84	0.74–0.95	0.92	0.90–0.94	0.97	0.96–0.98	0.63	0.55–0.74	0.03	0.00–0.05
Grey-headed albatross	1.04	1.03–1.05	0.83	0.71–0.96	0.91	0.87–0.94	0.96	0.95–0.97	0.65	0.55–0.74	0.03	0.00–0.05
Giant petrel	1.05	1.04–1.06	0.82	0.71–0.93	0.88	0.85–0.92	0.93	0.92–0.94	0.85	0.80–0.90	0.03	0.00–0.05
Black petrel	1.06	1.05–1.07	0.73	0.50–0.91	0.87	0.80–0.93	0.93	0.91–0.95	0.82	0.74–0.90	0.03	0.00–0.06
Flesh-footed shearwater	1.07	1.06–1.08	0.85	0.77–0.93	0.89	0.86–0.92	0.93	0.92–0.94	0.83	0.71–0.94	0.03	0.00–0.06
Common diving-petrel	1.08	1.07–1.09	0.73	0.65–0.83	0.77	0.70–0.84	0.86	0.83–0.89	0.87	0.80–0.94	0.04	0.00–0.07
Fairy prion	1.08	1.07–1.09	0.81	0.71–0.90	0.86	0.81–0.90	0.90	0.88–0.92	0.88	0.81–0.95	0.04	0.00–0.07
Storm petrel	1.09	1.08–1.10	0.75	0.70–0.84	0.83	0.80–0.88	0.91	0.90–0.92	0.85	0.80–0.94	0.04	0.00–0.07
Erect-crested penguin	1.16	1.15–1.17	0.73	0.57–0.86	0.82	0.75–0.88	0.88	0.84–0.90	0.81	0.71–0.90	0.04	0.00–0.09
Yellow-eyed penguin	1.16	1.15–1.17	0.71	0.54–0.88	0.82	0.75–0.90	0.90	0.87–0.92	0.75	0.61–0.89	0.04	0.00–0.09
Shag	1.19	1.18–1.20	0.76	0.70–0.86	0.83	0.80–0.88	0.89	0.88–0.90	0.82	0.75–0.93	0.05	0.00–0.09
Caspian tern	1.22	1.21–1.23	0.79	0.71–0.89	0.84	0.80–0.89	0.90	0.89–0.91	0.87	0.80–0.94	0.05	0.00–0.10

For each accepted sample, the strength of the density dependence C_{DD} (see Section 2.2) was uniformly sampled from values between 10^{-7} and 10^{-5}, on the logarithmic scale. This range of C_{DD} allowed the carrying capacity to vary between a few hundreds to several hundreds of thousands of individuals. The class-specific vulnerabilities to human-caused mortality (v_I, v_M, v_F for immatures, adult males, and adult females, respectively) were drawn randomly from a uniform distribution between 1 and 2, corresponding with all possibilities of one class being from half to twice as likely as the others to be killed by anthropogenic factors. An initial population proportion (p_K) was drawn from a uniform distribution between 0.05 and 1. This population proportion determined the initial population size as a proportion of the carrying capacity.

2.5 Calculating the maximum mortality rate, MMR

For each sample of the parameters, the carrying capacity was calculated by running 5000 simulations for 200 years, with no human-caused mortality. In subsequent simulations, the population was then

initialised at a proportion p_K of the carrying capacity, with the population structure set to the stable age distribution given by the right eigenvector of the transition matrix described in Equation 6 (Caswell 2001). Human-caused mortality was then applied from the first year, as a proportion of the number of birds in each class (immatures, adult male, and adult female, see 2.1). The maximum mortality rate, MMR, was determined by running 1000 trajectories and recording the proportion of the trajectories above $K/2$ after 200 simulated years, under various levels of human-caused mortality. A hunt-and-bisection search algorithm (Press et al. 2007) was used to determine the MMR, consisting of an initial hunt phase starting at a small human-caused mortality, and then multiplying it at each step by 2 until fewer than 95% of the population trajectories were above $K/2$. The MMR was subsequently obtained by dividing the human-caused mortality during a bisection phase, until sufficient precision was achieved (five significant digits).

2.6 Calculation of the Potential Biological Removal, PBR

The maximum growth rate, $r_{\max}$, is typically unknown, as it represents the rate of increase under optimal conditions and is, therefore, difficult to measure empirically. Niel & Lebreton (2005) calculated an approximation, $r_{\max}^{NL}$, for birds by assuming constant adult survival and fecundity after the age at first reproduction. They used the formulae:

$$\lambda_{\max}^{NL} = \exp\left[\left(A + \frac{S_A}{\lambda_{\max}^{NL} - S_A}\right)^{-1}\right] \tag{8}$$

$$r_{\max}^{NL} = \lambda_{\max}^{NL} - 1, \tag{9}$$

where A is the age at first reproduction, S_A the adult annual survival, and $\lambda_{\max}^{NL}$ is an approximation to the maximum annual population growth rate, i.e., without limiting factors.

This approach, used in Richard et al. (2011) and in other previous studies (Dillingham & Fletcher 2008, Waugh et al. 2009, Dillingham 2010, Dillingham & Fletcher 2011), assumes that the life history parameters of a species reflect the evolutionary trade-offs between productivity, survival, and age at first reproduction. Whereas small organisms generally show early maturity, low survival, and high productivity, larger organisms are characterised by delayed maturity, high survival, and low productivity. This trade-off between productivity and survival is formally expressed in the theory that the maximum growth rate per generation is constant among species. This theory was supported by Niel & Lebreton (2005)'s research of 13 bird species across 10 families, covering a large range of body weights, in conditions close to optimal (e.g., following reintroduction under complete protection, or during invasion processes). As a consequence, underestimates of A and S_A lead to overestimation of the approximation of the maximum annual population growth rate, i.e., $r_{\max}^{NL} > r_{\max}$.

For seabirds, most population estimates are derived from population surveys where only the adults breeding in a given year are counted. The proportion of the total population represented by these breeding pairs is generally unknown, as immature individuals are typically not counted, as they are oceanic for several years before returning to colonies as pre-adults. At the same time, not every adult breeds every year.

For this reason, following the method developed by Gilbert (2009) and Richard et al. (2011), we calculated an approximation of the population size, N^G to the total number of individuals greater than one year old (i.e., the individuals susceptible to captures in fisheries), N, using the formula:

$$N^G = \frac{2N_{\mathrm{BP}}}{P_B} S_A^{1-A}, \tag{10}$$

where N_{BP} is the number of annual breeding pairs, P_B the proportion of adults breeding in any given year, S_A the adult annual survival, and A the age at first reproduction. This equation assumes that the survival is constant after the first year.

Using Equations 3, 8, and 10, the calculation of PBR_b^* depends on four demographic parameters only: the number of annual breeding pairs (N_{BP}), the proportion of adults breeding in any given year (P_B), the adult annual survival rate (S_A), and the age at first reproduction (A). For each species type, we estimated a calibration factor, ρ, so that ρPBR_b^* does not exceed the maximum mortality (see Equation 2), for 95% of the parameter samples from each population. The base PBR is then $\text{PBR}_b = \rho \text{PBR}_b^*$, and the PBR may be calculated as:

$$\text{PBR} = \frac{1}{2} \rho \, r_{\text{max}}^{NL} N_{\text{min}}^G f. \tag{11}$$

2.7 Setting the recovery factor, f

Simulations were run to help guide choice of the recovery factor, f. We tested the robustness of the base PBR relative to the management criterion by considering the effect of errors in the four demographic parameters used in the base PBR calculation. These calculations allow the choice of recovery factor, f, to be guided by a consideration of how the base PBR is affected by different errors in the underlying parameters (Lonergan 2011).

Estimates of the demographic parameters are always uncertain, and may be biased. The adult survival rate (S_A) estimated from field data is most likely to be lower than the intrinsic rate (i.e., the natural survival without human-caused mortality), leading to an overestimation of r_{max} from the formula of Niel & Lebreton (2005). Some degree of human impact may be expected in most if not all seabird populations, although the reduction in survival due to anthropogenic factors is difficult to assess, and the natural survival rate may be impossible to estimate. Moreover, methods for estimating survival typically consider permanent emigration as equivalent to mortality and tend to produce under-estimates of survival, as does inappropriate modelling of detection probabilities in capture-recapture methods (Lebreton et al. 1992).

Estimates of age at first reproduction (A) may also be biased. To obtain correct estimates for mean values of this parameter, the age at first reproduction of all adults in the population needs to be recorded. The short-term nature of most studies, however, and the long period of time between the marking of individuals (before fledging) and their first reproduction in many seabirds often prevents the recording of the first age of reproduction of late breeders. In this case, A would be biased low. The relationship between A and the resulting PBR_b^* is non-linear. A low estimate of age at first reproduction A leads to a high estimate of r_{max}^{NL}, but a low estimate of N^G. Depending on the species, and the extent of the error, a low estimate of A may result in either a low or a high PBR_b^*.

For many species, there is also considerable uncertainty in the estimates of population size. Because most seabird populations are difficult to study due to the remoteness and inaccessibility of their colonies, estimates of the number of breeding pairs (N_{BP}) may be from outdated surveys that no longer reflect the current population status. For this reason, Wade & Angliss (1997) argued that population estimates older than 8 years should not be used, as a population decline of 10% annually starting at the carrying capacity K may lead to the population being at $K/2$ after 8 years. In the absence of recent estimates, however, older estimates may be used, including consideration of halving the available estimate to account for the potential population decline that may have occurred since the value was derived.

The probability of an adult breeding in a given year (P_B) is known only for a few species. Typical values used for this population parameter in the risk assessment of Richard et al. (2011) included 0.9 for species breeding annually, 0.6 for biennial species, and 0.75 for partially biennial species. As this parameter is used to estimate the adult population size from the number of breeding pairs, inaccurate estimates (e.g., owing to the lack of data) result in errors in estimates of the latter demographic parameter also. For example, using an estimate of P_B that is two thirds of the real value would lead to a large overestimate of the total population size.

We examined the consequence of such biases by varying each parameter independently between the value used for the simulations, and a value considered as a worst-case bias value: 90% of natural adult survival; 80% or 120% of the real value of the age at first reproduction (depending on the other parameters either an increase or a decrease in A may cause the PBR to decrease); twice the current number of annual breeding pairs; and two thirds of the probability of breeding. We calculated the value of the recovery factor, f, required for the population to still meet the management criterion in the presence of input parameter biases at these levels.

We also considered the effect of additional stochasticity. The base calculations were carried out by drawing samples, so that the c.v. of N in the sample populations was uniformly distributed between 0 and 0.2, with a mean of 0.1. A high-stochasticity case was considered by only accepting samples with the stochasticity in the upper quartile of the range, between 0.15 and 0.2. The high-stochasticity samples had a mean stochasticity of 0.175, an increase of 75% over the base case.

3. RESULTS

3.1 Maximum human-caused mortality rate, MMR

The MMR derived by simulations was lowest for large, long-lived species, and highest for small species with high productivity (Figure 4). For albatrosses, it was less than 2% of the total population annually, whereas for terns, it was around 10% annually. The values of the MMR were loosely bounded above by $\frac{1}{2}r_{\max}$ (Figure 5), where $r_{\max}$ was defined as $\lambda_{\max} - 1$. Under a deterministic logistic growth model, with no stochasticity, it follows that MMR $= \frac{1}{2}r_{\max}$. The difference between the MMR and $\frac{1}{2}r_{\max}$ was smallest for short-lived species, with a mean MMR around 97% of $\frac{1}{2}r_{\max}$ for diving petrels, and around 85% for albatrosses.

The deviation of MMR from $\frac{1}{2}r_{\max}$ was primarily driven by environmental stochasticity, and became greater with increasing environmental stochasticity (evident in the decreasing value of the ratio of MMR to $\frac{1}{2}r_{\max}$) (Figure 6). There was an approximately linear relationship between the stochasticity specified in the model (as the standard deviation in the survival rates), and the variation in the populations at the end of the simulations (measured through the c.v.). At the highest levels of stochasticity considered, the c.v. in the population was 0.2. This c.v. value was reached by a smaller standard deviation in survival rates for species with higher mean survival rates. At the higher values of the environmental stochasticity considered, MMR decreased to around $\frac{1}{4}r_{\max}$. The decrease was caused by populations being more likely to be below $K/2$ under conditions with higher environmental stochasticity. If the environmental stochasticity increased further, then MMR would continue to decrease. Under conditions of high stochasticity, it is possible that the management criterion would not be satisfied, even if there was no human-caused mortality. Even in the absence of human-caused mortality, more than 5% of the simulated populations could be less than $K/2$.
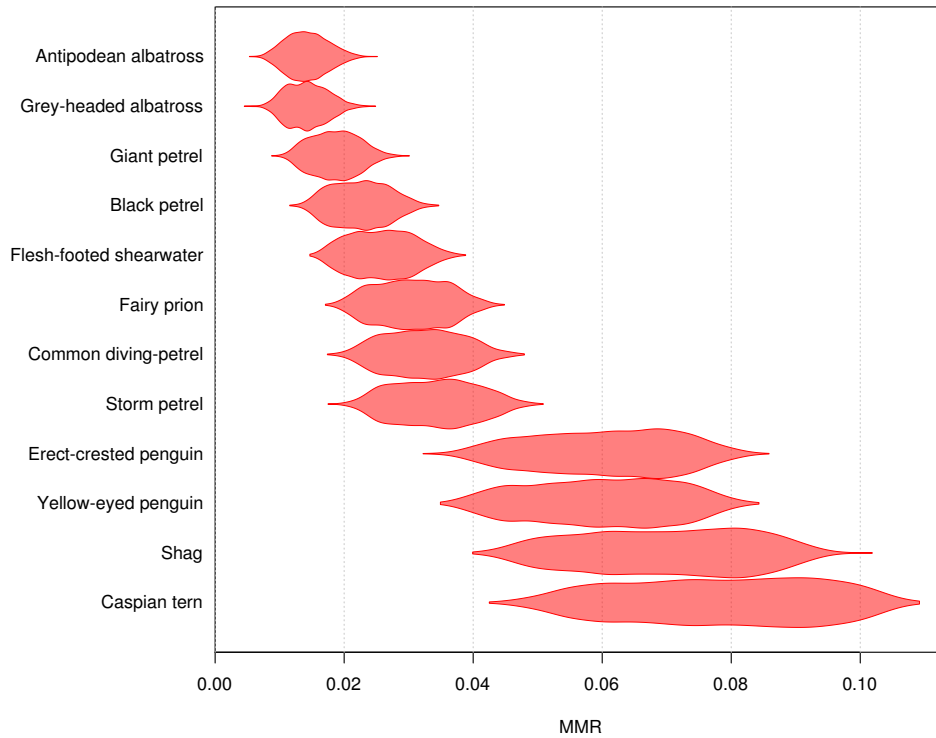
Figure 4: Distribution of the maximum human-caused mortality rate (MMR), the annual proportional mortality that would cause the population to just meet the management criterion, for each seabird type.
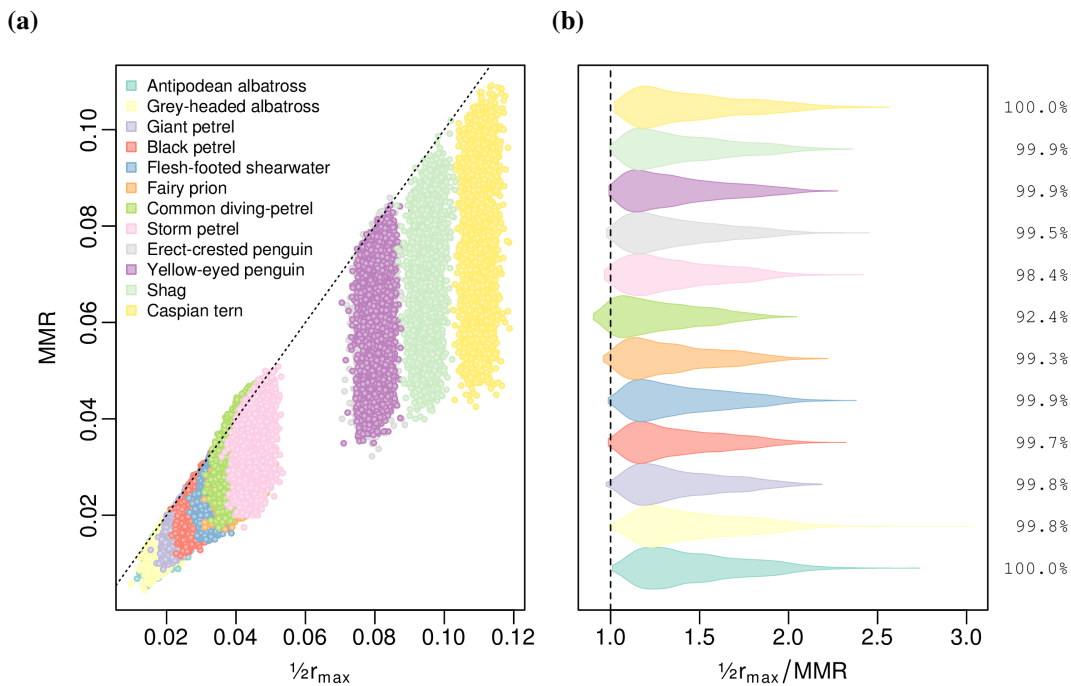
(a)

(b)

Figure 5: (a) Correlation between the maximum human-caused mortality rate (MMR) derived by simulations, and $\frac{1}{2}r_{max}$, the theoretical value under a logistic model, coloured by species type. (b) Distribution of the ratio of $\frac{1}{2}r_{max}$ to MMR for each species type, including the percentage of the distribution that is greater than 1 (values on right-hand axis).
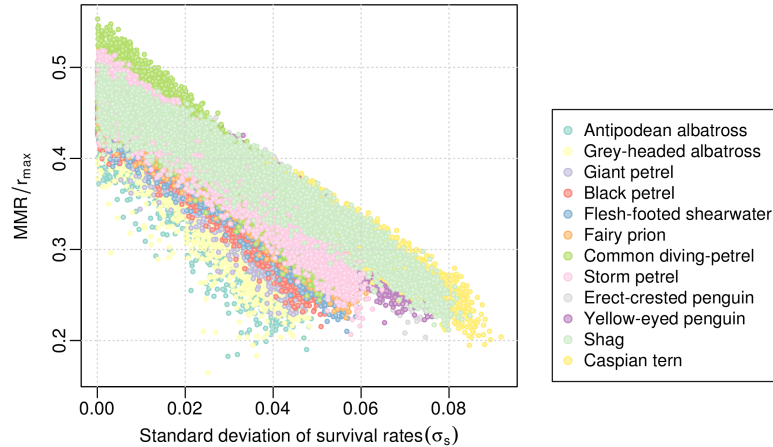
Figure 6: Variation in the ratio of the maximum human-caused mortality rate (MMR) to the maximum growth rate ($r_{\max}$) in relation to environmental stochasticity, for each of the species types. The stochasticity was specified in the model by the standard deviation in the survival rates (σ_S).

3.2 PBR calculation

3.2.1 Estimated maximum growth rate

We tested how well the approximation used for estimating the maximum growth rate compared with the value specified for each species type. The approximated maximum growth rate $r_{\max}^{NL}$, calculated following Niel & Lebreton (2005)(see Equation 3) from the parameters in Table 2, was generally higher than the values of $r_{\max}$ used for parametrising the simulations, except for terns (Figure 7 and Table 3). Among species laying only one egg per clutch, $r_{\max}^{NL}$ particularly overestimated $r_{\max}$ for short-lived species, with $r_{\max}^{NL}$ being around four times $r_{\max}$ for small species such as diving-petrels (Table 3). The Niel & Lebreton (2005) calculation was sensitive to small changes in the input parameters when the adult survival and the age of first reproduction are both low (Figure 8). Within species, $r_{\max}^{NL}$ increased with increasing relative population size, because the adult survival rate and the probability of breeding both decrease when the population increases towards carrying capacity.

3.2.2 Estimated total population size

The mean ratio of the total population size to the number of annual breeding pairs from the demographic model (N/N_{BP}) varied from 3.11 for species like diving petrels to 8.32 for biennially breeding albatrosses (Table 4), similar to the population multipliers found by Dillingham & Fletcher (2011) (around 5 for annually breeding petrels and albatross, and around 11 for biennially breeding albatrosses). The ratios were larger than those used elsewhere, e.g., 5 for biennial species and 4 for annual species as in Waugh et al. (2012), and 3 as in Brooke (2004), or the different ratios in Robertson & Gales (1998), which were decided based on expert knowledge at that time (R. Gales, pers. comm.).

The ratio of the total population size to the number of adults from the demographic model (N/N_A) varied between 1.29 and 2.53, consistently exceeding the values calculated following Gilbert (2009). When the ratio of the total population size to the number of annual breeding pairs was calculated following Gilbert (2009), N^G/N_{BP} also consistently underestimated N/N_{BP}, except for some samples of biennial albatrosses (Figure 9). This underestimation was greater for species with high survival rates and low probability of breeding. Using the estimate of total population size following Gilbert (2009) would
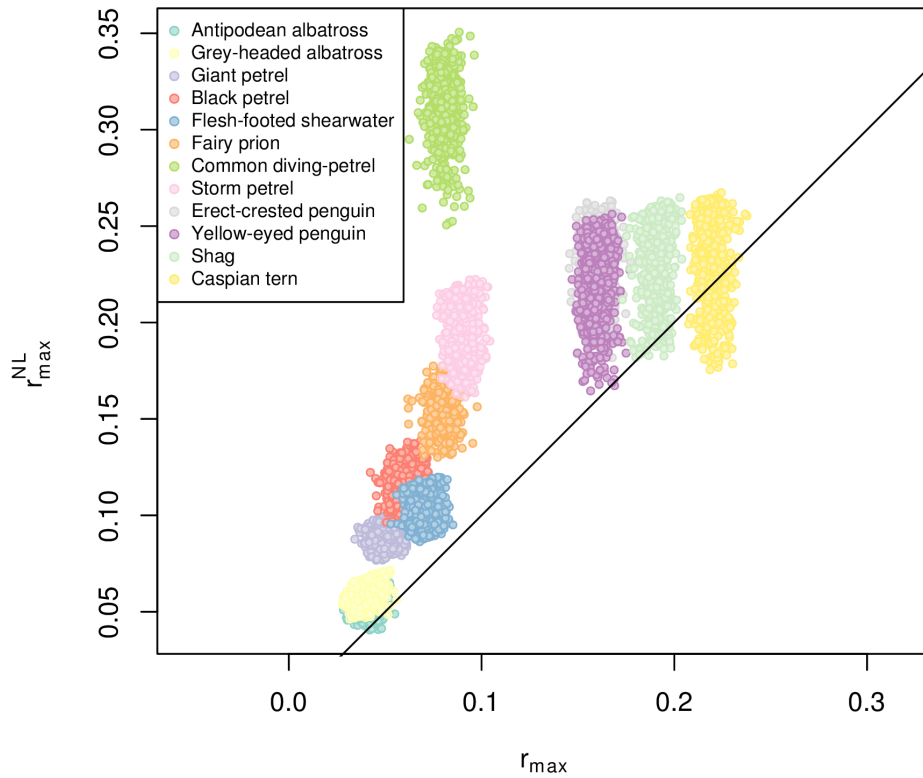
Figure 7: Relationship between the maximum growth rate r_{max}^{NL} estimated using the Niel & Lebreton (2005) method, and the r_{max} value used to drive the simulations, coloured by species type.

Table 3: Maximum growth rate for the different types of seabird species breeding within New Zealand's Exclusive Economic Zone. Mean and 95% confidence interval of values used in the simulations, r_{max}, and the estimates following Niel & Lebreton (2005), r_{max}^{NL}.

| Species type	r_{max}		r_{max}^{NL}		r_{max}^{NL}/r_{max}	
	Mean	95% c.i.	Mean	95% c.i.	Mean	95% c.i.
Antipodean albatross	0.04	0.03–0.05	0.05	0.04–0.06	1.36	0.98–1.79
Grey-headed albatross	0.04	0.03–0.05	0.06	0.05–0.07	1.50	1.12–1.92
Giant petrel	0.05	0.04–0.06	0.09	0.08–0.10	1.81	1.44–2.23
Black petrel	0.06	0.05–0.07	0.12	0.10–0.13	1.96	1.55–2.42
Flesh-footed shearwater	0.07	0.06–0.08	0.11	0.09–0.12	1.50	1.22–1.79
Fairy prion	0.08	0.07–0.09	0.16	0.13–0.17	1.95	1.61–2.30
Common diving petrel	0.08	0.07–0.09	0.31	0.27–0.34	3.88	3.19–4.58
Storm petrel	0.09	0.08–0.10	0.20	0.17–0.22	2.17	1.80–2.55
Erect-crested penguin	0.16	0.15–0.17	0.23	0.19–0.26	1.42	1.17–1.63
Yellow-eyed penguin	0.16	0.15–0.17	0.22	0.18–0.25	1.36	1.10–1.59
Shag	0.19	0.18–0.20	0.23	0.19–0.26	1.21	0.99–1.38
Caspian tern	0.22	0.21–0.23	0.23	0.18–0.26	1.04	0.83–1.21
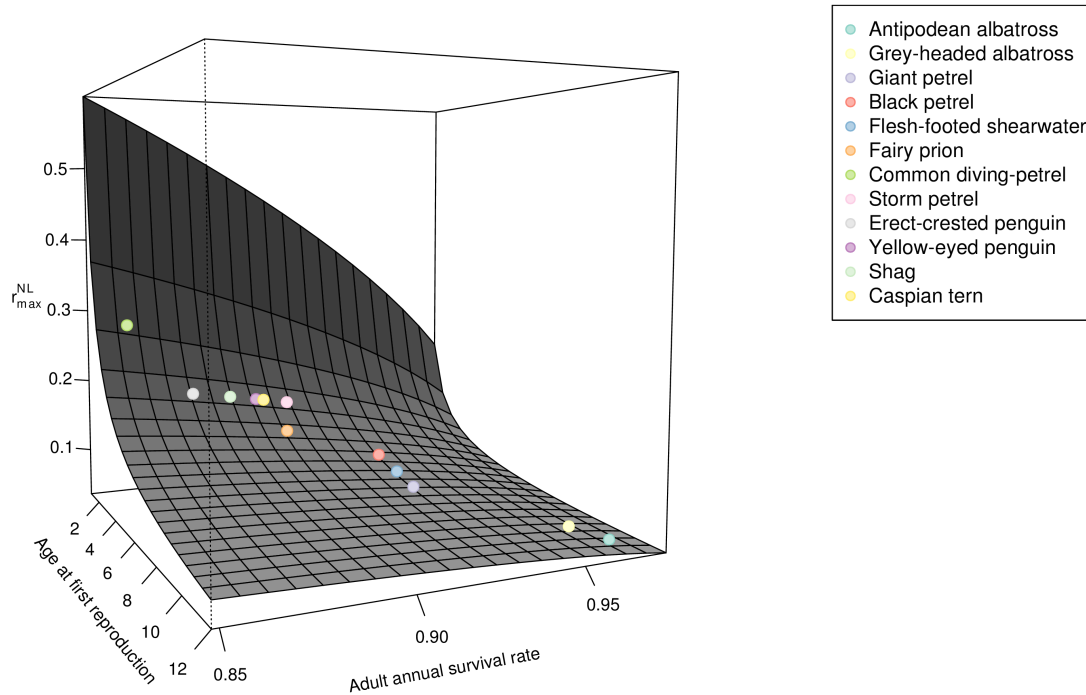
Figure 8: Relationship between r_{max}^{NL} calculated following Niel & Lebreton (2005) and the two parameters used to calculate it: the age at first reproduction and the adult annual survival rate. The points on the surface show the mean value for each type of seabird species.

result in a lower estimate of the PBR, which would result in fisheries mortalities at the PBR being less likely to impact the population.

Within species, the deviation of N^G/N_{BP} from N/N_{BP} was mainly driven by the relative population size. This finding resulted from density dependence in the model leading to a decrease in the adult survival rate, which in turn increased the ratio of the total population size to the number of adults when applying the Gilbert (2009) formula (Figure 10). In the model, density dependence also led to a decrease in the probability of breeding and, therefore, in the ratio of the number of adults to the number of breeding pairs, as $N_A = 2N_{BP}/P_B$.

3.3 Correcting the estimated Potential Biological Removal, PBR

Without correction, PBR_b^* exceeded the maximum human-caused mortalities (MM) with a probability higher than 5% for all species types (Figure 11). The overestimation was largest for diving petrels, due to a high r_{max}^{NL} (see Figure 7) and a higher population multiplier on average (see Figure 9). For this species type, PBR_b^* may exceed MM by a factor of over 3. The smallest overestimation was found for terns, for which only 7.7% of the values of PBR_b^* were greater than MM.

The calibration factor ρ was 0.17 for species like common diving petrels (Table 5), but was between 0.3 and 0.4 for most other single-egg clutch species types, and around 0.5 to 0.6 for species laying two eggs. The probability that PBR_b exceeds the mortality limit is sensitive to the value of ρ. Species like common diving petrels represent the most extreme case, with a change of ρ from 0.1 to 0.4 causing this probability to change from 0% to 100%.

Table 4: Ratio of the total population size to the number of adults from the demographic model, N/N_A, and following Gilbert (2009), N^G/N_A, and ratio of the total population size to the number of annual breeding pairs from the demographic model, N/N_{BP}. The estimates are presented as means and 95% confidence intervals for the different types of seabird species breeding within New Zealand's Exclusive Economic Zone.

| Species type	N/N_A		N^G/N_A		N/N_{BP}	
	Mean	95% c.i.	Mean	95% c.i.	Mean	95% c.i.
Antipodean albatross	2.53	2.30–2.82	2.04	1.41–2.96	8.32	7.30–9.39
Grey-headed albatross	2.43	2.21–2.68	1.97	1.43–2.76	7.81	6.78–8.89
Giant petrel	2.33	2.18–2.48	1.98	1.56–2.52	5.72	5.24–6.24
Black petrel	1.85	1.63–2.04	1.58	1.31–1.93	4.70	3.99–5.38
Flesh-footed shearwater	2.18	2.03–2.33	1.90	1.46–2.44	5.57	4.92–6.30
Fairy prion	1.80	1.70–1.90	1.60	1.35–1.87	4.32	3.91–4.76
Common diving petrel	1.29	1.25–1.34	1.21	1.15–1.28	3.11	2.84–3.40
Storm petrel	1.51	1.47–1.56	1.35	1.23–1.49	3.75	3.41–4.08
Erect-crested penguin	1.86	1.70–2.00	1.59	1.31–1.91	5.10	4.29–6.00
Yellow-eyed penguin	1.78	1.64–1.93	1.51	1.26–1.80	5.28	4.21–6.52
Shag	1.89	1.81–1.96	1.61	1.31–1.92	5.21	4.48–5.98
Caspian tern	1.94	1.85–2.03	1.62	1.28–1.99	5.12	4.39–5.92

(a) **(b)**
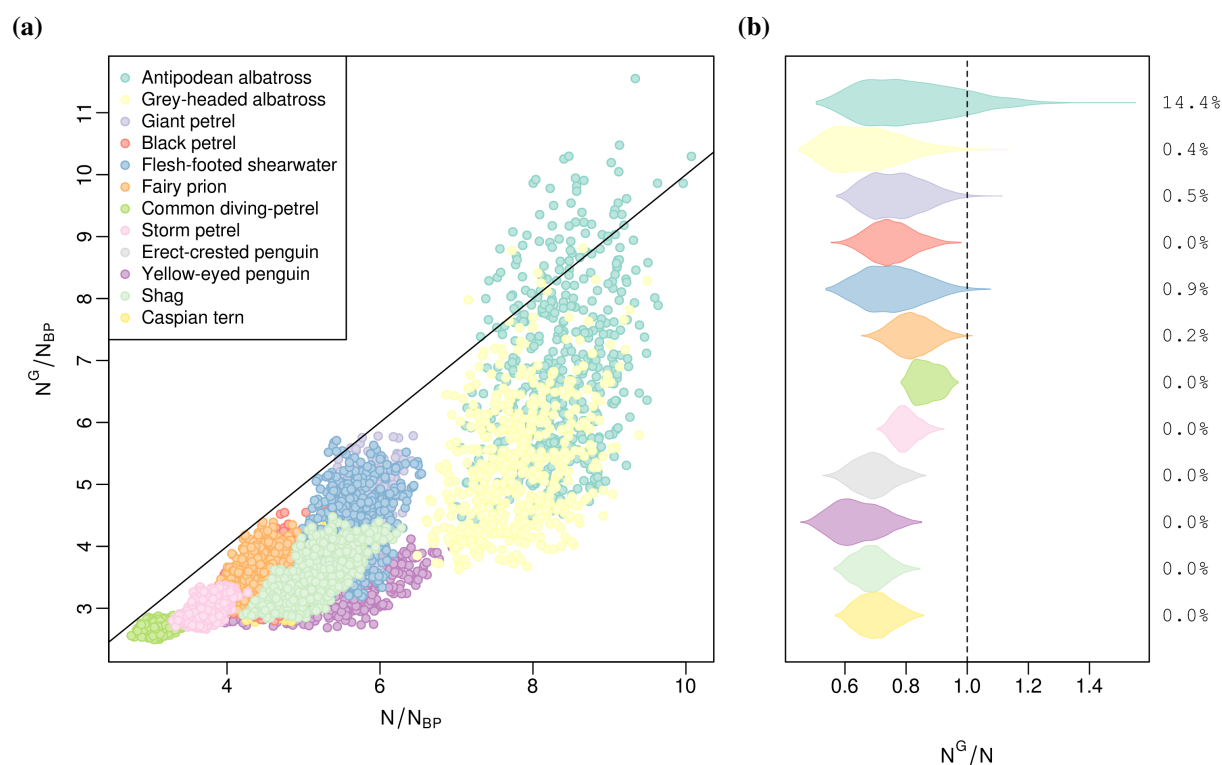
Figure 9: (a) Relationship between the ratio of the total population size to the number of breeding pairs N^G/N_{BP} calculated following Gilbert (2009) and the ratio from the simulations N/N_{BP}; and (b) distribution of the ratio of N^G to N for each species type, along with the probability that $N_G > N$.
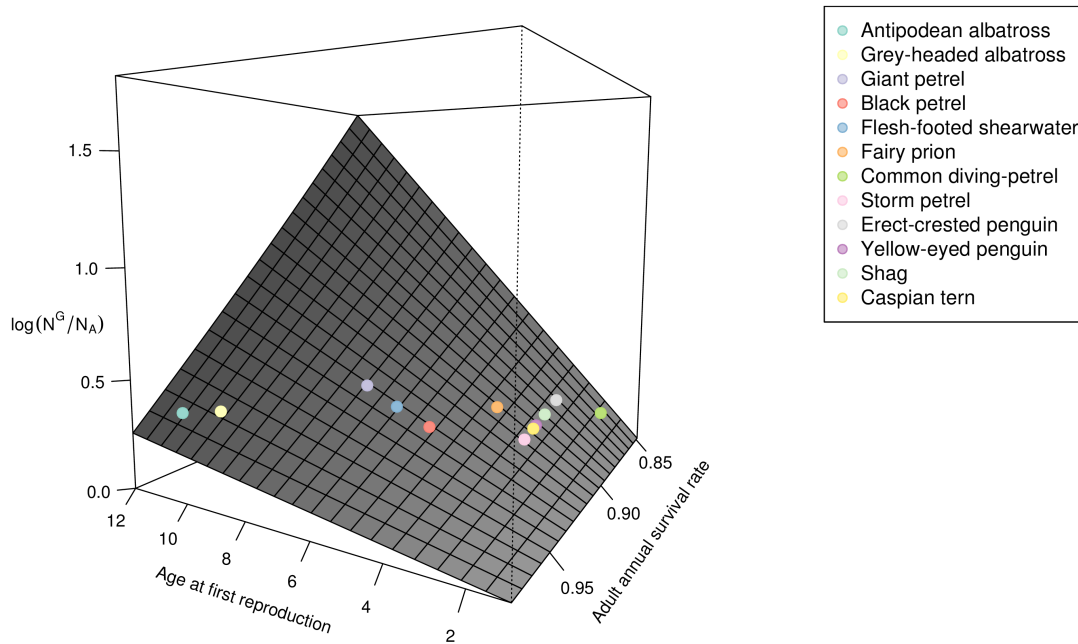
Figure 10: Relationship between the ratio of the total population to the number of adults N^G/N_A calculated following Gilbert (2009) and the two parameters used to calculate it: the age at first reproduction and the adult annual survival rate. The points on the surface show the mean value for each type of seabird species.
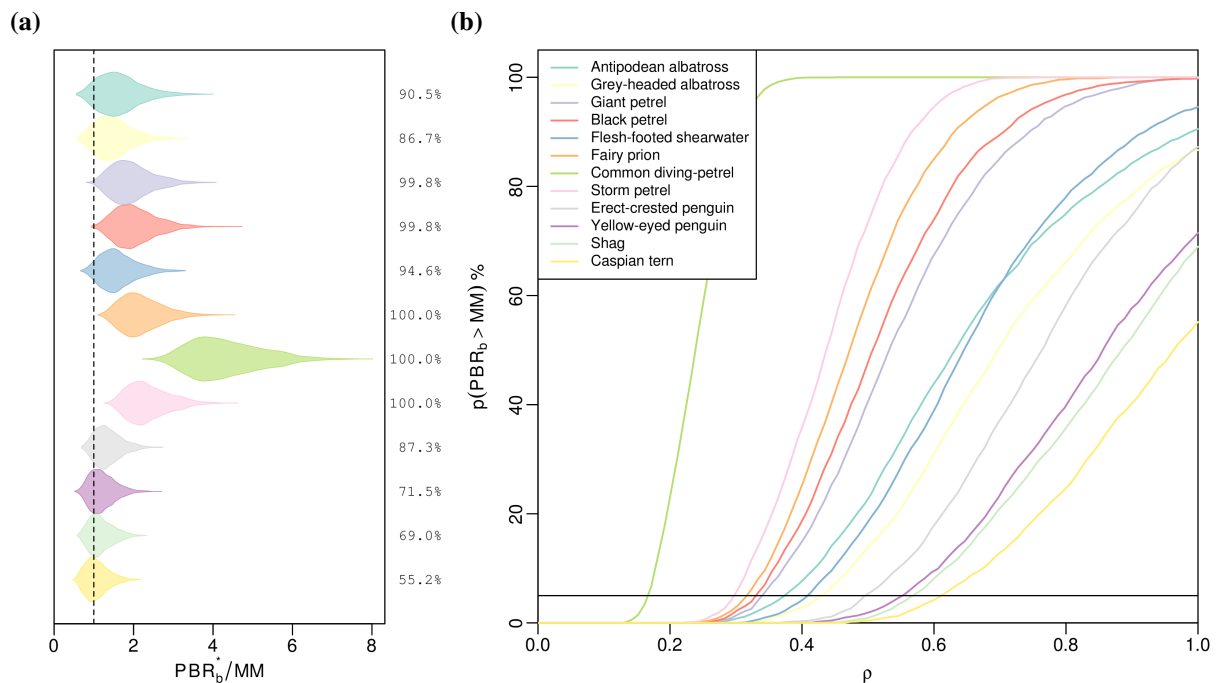
(a)

(b)

Figure 11: (a) Distribution of the ratio of PBR_b^* (estimated base Potential Biological Removal) to the maximum human-caused mortality (MM) for each species type; and (b) probability that $\mathrm{PBR}_b > \mathrm{MM}$, as a function of the correction factor ρ. The horizontal line marks the line where the management criterion is just satisfied, and PBR_b has only a 5% probability of being greater than MM.

Table 5: Correction factor (ρ) so that the Potential Biological Removal (with recovery factor $f = 1$) does not exceed the maximum human-caused mortality, $\text{PBR}_b < \text{MM}$, for 95% of simulated populations.

Species type	ρ
Antipodean albatross	0.37
Grey-headed albatross	0.43
Giant petrel	0.34
Black petrel	0.33
Flesh-footed shearwater	0.41
Fairy prion	0.32
Common diving petrel	0.17
Storm petrel	0.30
Erect-crested penguin	0.50
Yellow-eyed penguin	0.55
Shag	0.57
Caspian tern	0.61

3.4   Adjustment of f

We introduced errors into the estimates of the demographic parameters to test the sensitivity of the PBR, and to inform selection of an appropriate recovery factor, f, on a case-by-case basis to account for expected or plausible levels of bias. The PBR appeared to be most sensitive to errors in the adult annual survival rate S_A (Figure 12). This effect was greater for long-lived species, because of the multiplicative effect of the bias. When a 90% reduction was applied to the adult survival, a rate of 0.95 reduced to 0.86, corresponding to a decrease in longevity ($1/(1 - S_A)$) from 20 years to less than 7 years. In contrast, an adult survival of 0.70 decreased to 0.63, corresponding to a relatively small change of longevity from 3.3 to 2.7 years. Given that most published estimates of adult survival rates for albatrosses are over 90%, the error in the adult survival must be less than the 10% maximum considered here. There are some exceptions, such as Chatham and Gibson's albatrosses for which annual survival has been estimated at 86.8% (Robertson et al. 2003) and 88.3% (Agreement on the Conservation of Albatrosses and Petrels (ACAP) 2010), respectively. In those cases natural survival is expected to be at least 95% (e.g., Elliott & Walker 2005).

The PBR is also sensitive to biases in the probability of breeding, P_B. When the value of P_B was lowered by one third, the resulting PBR_b exceeded the maximum human-caused mortality (MM) with a probability between 55% and close to 100%. The greatest effect was for the short-lived species, whereas the smallest effect was for long-lived species. When N_{BP} was tested at values of twice the original estimates, the resulting PBR_b exceeded MM with a probability of around 50% (between 39% and 79%).

The PBR is relatively insensitive to the age at first reproduction, A. When A was estimated at 80% of its initial value, PBR_b exceeded MM with a probability between 5% and 18%, with a higher effect for common diving-petrel and storm petrel. For the long-lived species, PBR_b increased relative to MM when A was increased by 120%, but the effect was not strong (the greatest increase was to a probability of 7.2% that PBR_b exceeded MM, for Antipodean albatross).

When combining biases in S_A, A, P_B, and N_{BP}, PBR_b exceeded MM on average by a factor between 2.2 for penguins and 4.4 for albatrosses. To ensure that under the considered biases the PBR remained below MM with a 95%-probability, the recovery factor f for each species type needed to be between 0.12 for albatrosses and 0.25 for shags and gulls (Table 6).

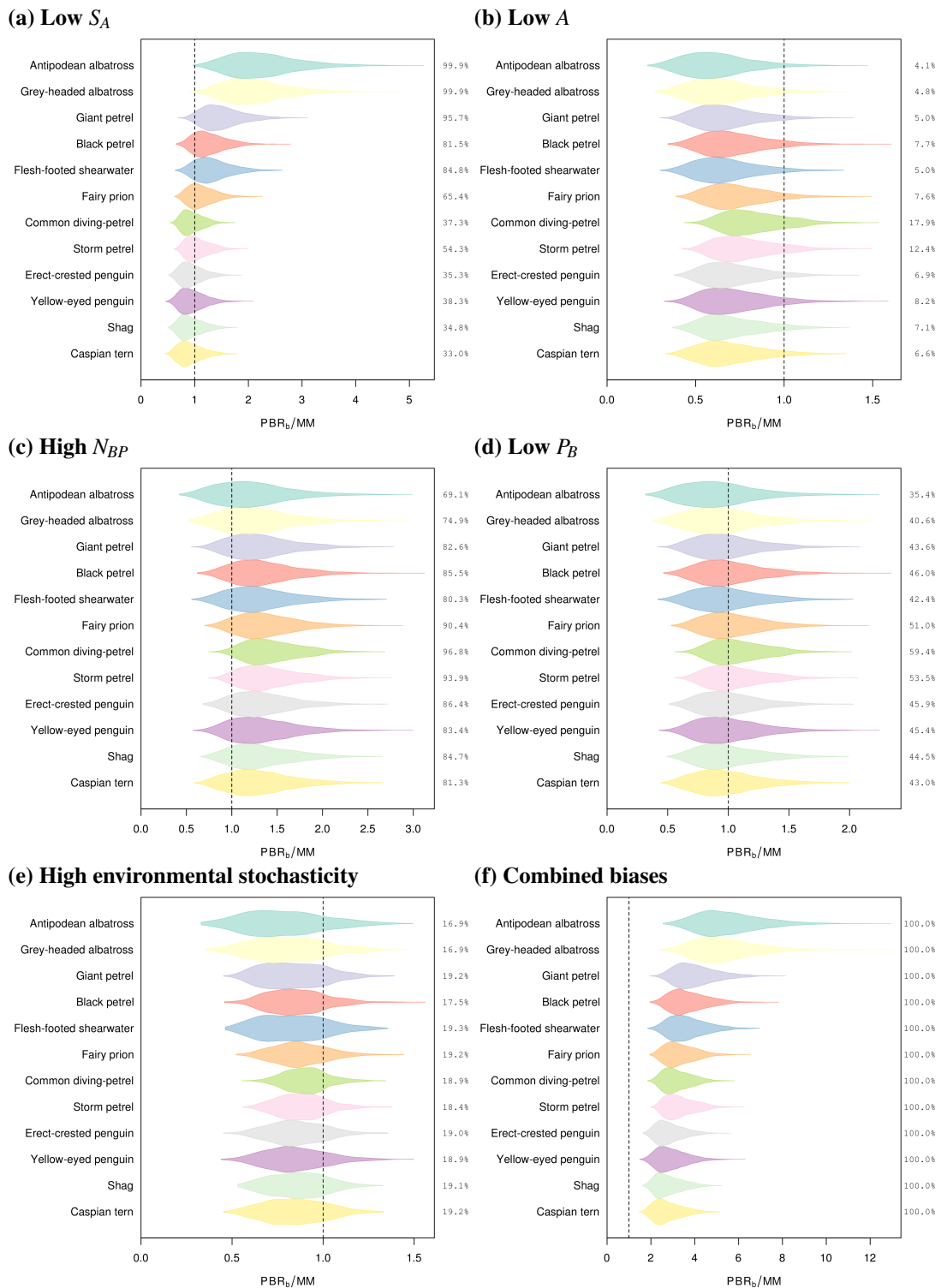An increase in the environmental stochasticity from a mean value of 0.100 to a mean value of 0.175

Figure 12: Ratio of PBR$_b$ (Potential Biological Removal, with recovery factor $f = 1$, and total population N), to the maximum human-caused mortality (MM) with different biases in the demographic parameters used for the PBR calculation (S_A, adult annual survival; A, age at first reproduction; N_{BP}, number of annual breeding pairs; P_B, proportion of adults breeding in any given year). The probability that PBR$_b >$ MM is shown on the right hand side of each plot.

Table 6: Appropriate recovery factors (f) to compensate for bias in the demographic parameters, such that the Potential Biological Removal does not exceed the maximum human-caused mortality (PBR$_b$ ≤ MM, with a 95% probability). Considered biases were: low S_A, 10% reduction in adult annual survival; low A, 20% reduction in age at first reproduction; high A, 20% increase in age at first reproduction; high N_{BP}, doubling in the number of annual breeding pairs; low P_B, one-third reduction in the proportion of adults breeding in any given year; combined biases, biases in S_A, A, N_{BP}, and P_B (with the bias in A being the one that leads to the lower appropriate f value); high stochasticity, 75% increase in mean population stochasticity.

Species type	Low S_A	Low A	High A	High N_{BP}	Low P_B	Combined biases	High stochasticity
Antipodean albatross	0.29	1.03	0.94	0.50	0.67	0.12	0.85
Grey-headed albatross	0.31	1.01	0.96	0.50	0.67	0.13	0.84
Giant petrel	0.45	1.00	0.96	0.50	0.67	0.17	0.87
Black petrel	0.54	0.96	1.01	0.50	0.67	0.19	0.88
Flesh-footed shearwater	0.51	1.00	0.96	0.50	0.67	0.19	0.87
Fairy prion	0.63	0.96	1.00	0.50	0.67	0.22	0.88
Common diving petrel	0.76	0.87	1.09	0.50	0.67	0.23	0.90
Storm petrel	0.68	0.91	1.06	0.50	0.67	0.22	0.88
Erect-crested penguin	0.73	0.96	1.01	0.50	0.67	0.25	0.90
Yellow-eyed penguin	0.72	0.94	1.01	0.50	0.67	0.24	0.87
Shag	0.73	0.97	0.99	0.50	0.67	0.25	0.89
Caspian tern	0.74	0.97	0.99	0.50	0.67	0.25	0.89

(measured by the c.v. of the population), resulted in an increase of the proportion of PBR$_b$ values greater than MM from 5% to between 17% and 20%. The increase was consistent across all species.

The values of f in Table 6 were calculated using fixed levels of bias in each of the demographic parameters. Figure 13 shows the appropriate value of f for a range of bias in the estimates of the demographic parameters. The relationship between the choice of f and the bias suggests that f is most sensitive to small levels of bias in the annual survival rate and in the number of breeding pairs, whereas small amounts of bias in the age at first reproduction have a minimal impact on the choice of f (Figure 13). The relationship is linear for the probability of breeding, indicating an equal sensitivity of f to this parameter, regardless of the amount of bias.

When calculating the PBR, the value of the recovery factor may be chosen to account for levels of bias in the estimation of the demographic parameters that are considered plausible. The choice of the recovery factor depends on the potential bias that is thought to exist in the parameter estimates on a case-by-case basis, and on the tolerance for risk, with lower f values protecting against larger (but less likely) biases. Wade (1998) considered that an f value of 0.5 was appropriate for this purpose when setting the PBR for marine mammals. For seabirds, biases in the number of breeding pairs are partly addressed by using a lower estimate of the population size, N_{min}, in the calculation of the PBR, rather than the total population size, N.

3.5 Time to recovery

In the absence of human-caused mortality, simulated populations starting at 5% of their habitat carrying capacity take between 17 years for Caspian tern and 78 years for Grey-headed albatross to reach half the carrying capacity (Table 7). When the annual human-caused mortality rate is MMR, the time to recovery for the same populations approximately doubles, to between 34 years for species like the Caspian tern and 169 years for species like the grey-headed albatross. For albatrosses, a recovery factor of f less than
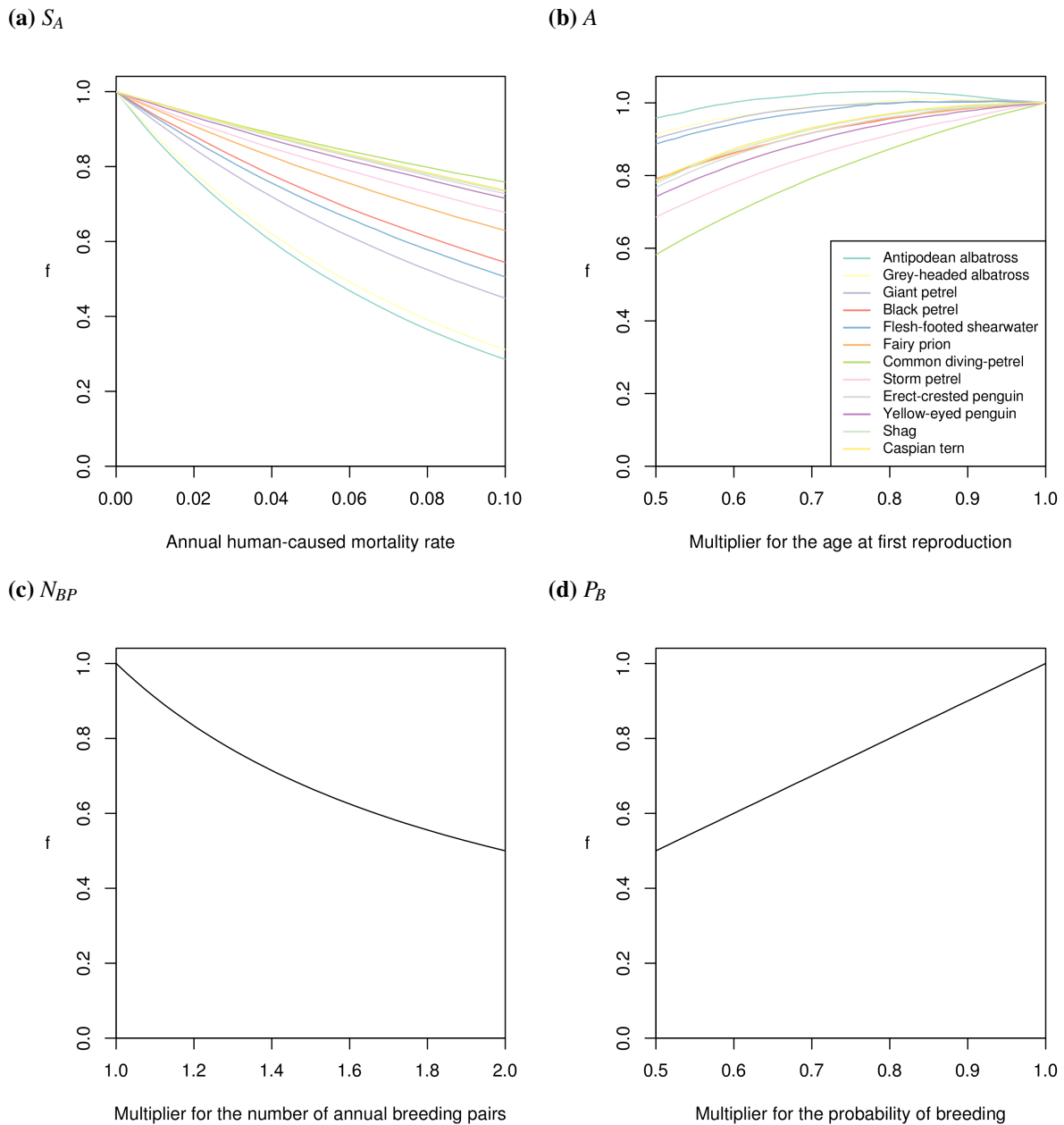
(a) S_A

(b) A

(c) N_{BP}

(d) P_B

Figure 13: Adjustment of the recovery factor f as a function of the level of bias in the demographic parameters so that the Potential Biological Removal (PBR) has a 95% probability of being less than the maximum human-caused mortality (MM): (a) adult annual survival S_A relative to annual human-caused mortality rate, (b) the estimated age at first reproduction A relative to the actual value, (c) the estimated number of annual breeding pairs N_{BP} relative to the actual value, and (d) the estimated probability of breeding P_B relative to the actual value. (In (a) and (b), the change in f depends on the species type, whereas the change is independent of species type in (c) and (d).)

one is required for the populations to be able to recover from 5% to over $K/2$ in less than 100 years. The relationship between the time to recovery and the annual human-caused mortality rate is monotonic and concave (Figure 14), indicating that a greater change in the time to recovery is achieved from the initial decrease of human-caused mortality below MMR. With a decrease of 50% in the annual human-caused mortality rate, from MMR to $\frac{1}{2}$MMR, the decrease in the time to recovery is between 31% for species like the Antipodean albatross to 40% for species like shags (Figure 14).

Table 7: Time to recovery (years) for a population starting at 5% of the carrying capacity, with different levels of human-caused mortality (HCM), expressed as a proportion of the maximum human-caused mortality rate (MMR). The demographic parameters for each species type were set to the mean of the values used in the simulations.

Species type	HCM (proportion of MMR)				
	0.1	0.25	0.50	0.75	1.0
Antipodean albatross	77	87	100	118	144
Grey-headed albatross	78	88	105	128	169
Giant petrel	63	72	84	100	128
Black petrel	52	59	69	84	114
Flesh-footed shearwater	46	52	60	72	90
Fairy prion	40	46	54	66	89
Common diving-petrel	40	45	52	64	82
Storm petrel	36	40	46	56	71
Erect-crested penguin	22	24	28	34	41
Yellow-eyed penguin	21	24	28	33	42
Shag	19	21	25	30	42
Caspian tern	17	18	22	26	34

3.6 Sensitivity to density dependence

In the simulations carried out to calibrate the PBR, a linear relationship was assumed between the density-dependent parameters and the population size. Values of the vital rate under density dependence θ higher than 1 (see Section 2.3) represent situations in which density dependence affects populations mainly at high density. As part of the analysis, simulations were run with values of θ between 1 and 5, while r_{max} was kept constant. As expected, when the θ value increased, the growth rate at the maximum net productivity level increased. Consequently, the maximum mortality rate increased (Figure 15). When $\theta = 5$, the maximum mortality was above twice the maximum mortality compared with $\theta = 1$. However, with a non-linear relationship between population size and growth rate, the population size decreased rapidly through $K/2$, leading to a population collapse when exceeding the MMR.

The functional form of the density dependence is not known for any of the seabird populations breeding within New Zealand waters; however, it is expected that simulations with $\theta > 1$ will be more representative of the actual population dynamics. In this case, the estimated PBR may be lower than the true MM (by a factor of between 2 and 3, if $\theta = 5$). Because of the steepening of the relationship between mortality and population size when the population size is around $K/2$ as θ increases, we recommend that the MMR is calculated assuming a linear relationship between population size and growth rate.
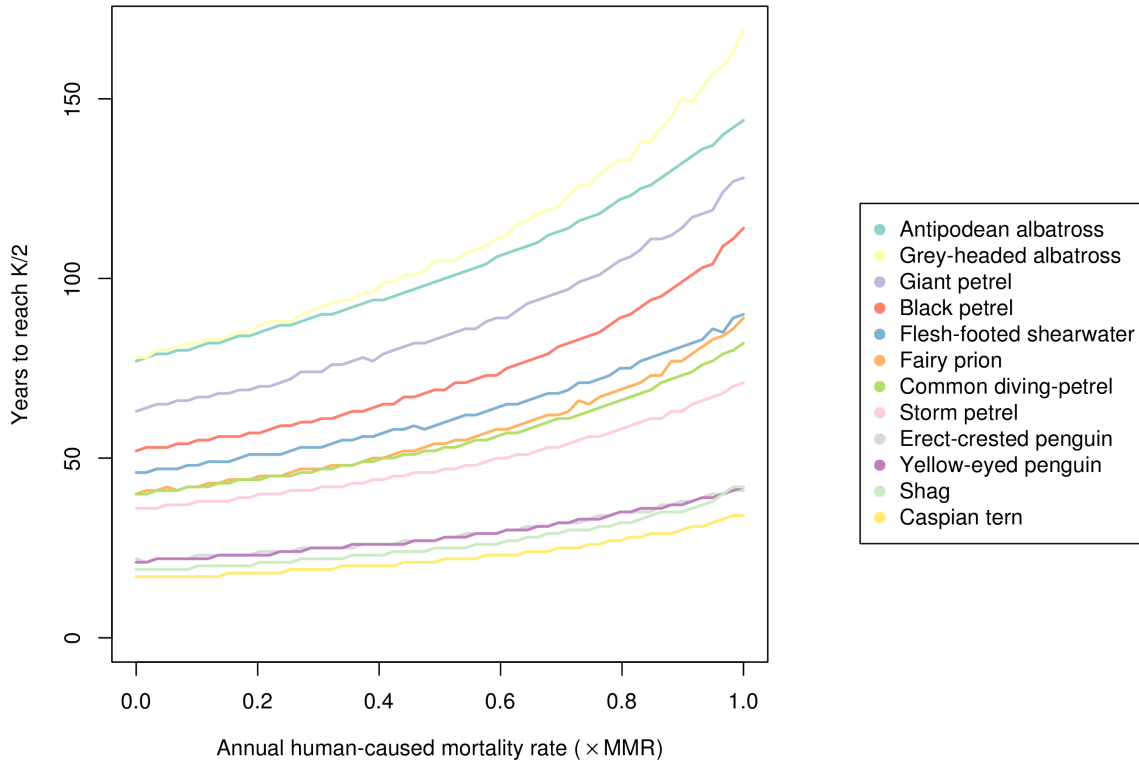
Figure 14: Time to recovery (years) for a population starting at 5% of the carrying capacity, with a human-caused mortality rate equal to fMMR, with f being the recovery factor, and MMR the maximum human-caused mortality rate. The demographic parameters for each species type were set to the mean of the values used in the simulations.
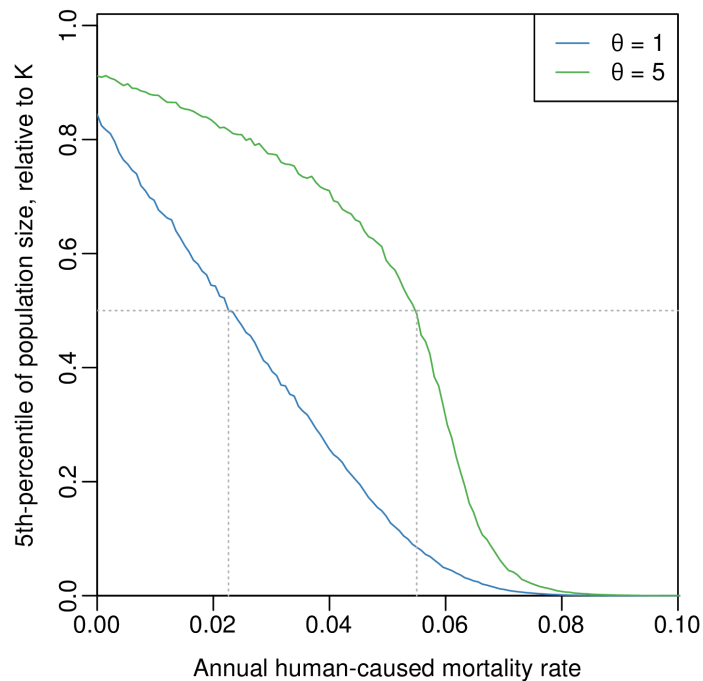

Figure 15: Effect of human-caused mortality on seabird population size, for two different values of the density-dependence parameter θ. The curves are from simulations of black petrel populations with $\theta = 1$ (linear dependence) and $\theta = 5$. K is the carrying capacity.

4. DISCUSSION

4.1 Application of the PBR to seabird populations

Using the results of this study, the PBR may be calculated using the following formula

$$\text{PBR} = \frac{1}{2}\rho r_{\max}^{NL} N_{\min}^{G} f, \tag{12}$$

where ρ values are taken from Table 5; $r_{\max}^{NL}$ is calculated using Equation 8 (Niel & Lebreton 2005); the population size is calculated using Equation 10 (Gilbert 2009); and the recovery factor is chosen on a case-by-case basis to adjust for potential errors or biases affecting the estimation of the base PBR, and possibly to reflect other management criteria.

The calibration factor, ρ, varied between 0.17 and 0.61 depending on the species type. The calibration factor primarily accounted for errors in the estimation of the maximum growth rate and the total population size. The calculation of the calibration factor ρ also reflected the inclusion of environmental stochasticity in the simulations (which had a mean value that resulted in the population having a c.v. of 0.1). In the absence of stochasticity, the maximum human-caused mortality rate (MMR) that allowed the population to meet the management criterion was close to $\frac{1}{2}r_{\max}$. As the environmental stochasticity increased, the MMR decreased, necessitating a lower calibration factor ρ. The equation above (Equation 12) was used in a recent risk assessment by Richard et al. (2011), without including the calibration factor ρ. All else being equal, the PBR values calculated in the previous risk assessment by Richard et al. (2011) would have been over-estimated by a factor of $1/\rho$ (i.e., between 1.6 and 5.9); however, by coincidence, the choice of recovery factor (ranging between 0.1 and 0.5) largely compensated for the errors derived from using the approximation methods.

To calculate the PBR following Equation 12, estimates are required for the number of breeding pairs, adult survival, the proportion of adults that breed in any given year, and the age at first reproduction. These parameters are all based on field observations, although the age at first reproduction and adult survival rate should ideally be measured when populations are not subject to strong density-dependence and human-caused mortality. In particular, if adult survival rate is suspected to be greatly affected by human-caused mortality, then it may be more appropriate to use survival estimates from closely related species.

Calculating the PBR using Equation 12, a minimum estimate for the number of breeding pairs should be taken when several estimates are available. In cases where there is a distribution of population sizes, Wade (1998) recommended using the lower 20th percentile of it. If a point estimate of the PBR is required, then the 20th percentile should also be used for the number of breeding pairs when calculating $N_{\min}^{G}$ for use in Equation 12. In Richard et al. (2011), uncertainty in the input parameters was carried through the calculation of the PBR, resulting in a distribution of PBR values. In this case, the lower quartile of the distribution of the number of breeding pairs was used. If the same procedure is used to calculate the PBR following Equation 12, then each sample from the resulting distribution will represent a calibrated PBR value. A point estimate for the PBR may be obtained from the median of the resulting PBR distribution.

When assessing a population relative to the PBR, the PBR should be compared with the total annual human-caused mortality, not only fishing-related mortality. Other anthropogenic factors affect seabirds, and some species may be in decline due to human-caused mortalities, even though the fishing mortality is less than the PBR. Comparing mortality to the PBR for each risk factor separately may lead to the perception that all sources of human-caused mortality are below the PBR and so are acceptable, even though the total human-caused mortality level may be above the PBR.

4.2 Choosing the recovery factor, f

The calibration factor, ρ, allows the base PBR to be estimated, based on perfect knowledge of the input parameters, including the age at first reproduction, adult survival, annual probability of an adult breeding, and the number of breeding pairs. When the PBR is applied to actual seabird populations, however, the parameters are only known imperfectly from field measurements. Following Wade (1998), potential values of the recovery factor f were assessed to ensure that the estimated PBR satisfies the management criterion, even when errors are present in the estimates of the demographic parameters. The bias calculation (reported in Table 6) may be used to guide the choice of f values, depending on an assessment of the scale of the potential errors. The choice of the recovery factor depends on the potential bias that is thought to exist in the parameter estimates, on a case by case basis, and on the tolerance for risk, with lower f values protecting against larger (but less likely) biases. Wade (1998) considered that an f value of 0.5 was appropriate for this purpose when setting the PBR for marine mammals.

Some of the potential error is already included in the application of the PBR through the use of a minimum estimate of the population size, N_{min}, rather than the population N used in calculating the base PBR. In addition, in probabilistic applications of the PBR (Richard et al. 2011), input parameters are represented as distributions, with associated uncertainty. This uncertainty is carried through the calculation, resulting in a distribution of PBR values. It is possible for plausible parameter biases to be already incorporated within the input distributions.

The recovery factor, f, may be reduced when a population is suspected to have been experiencing a large decline, so that its recovery should become a management priority. The stated management criterion (that after sufficient time the population should have a 95% probability of being above $K/2$) does not have an explicit goal of recovery time. In the application of PBR methods to marine mammals, the United States National Marine Fisheries Service (NMFS) requires an additional goal, that populations recovering from depletion (i.e., starting at below 30% of carrying capacity) have a 95% probability of being above $K/2$ in 100 years (Taylor et al. 2000). This explicit recovery time in turn requires that a lower recovery factor be included for long-lived species.

The choice of the f value is ultimately a management decision. In the application of the PBR to seabirds, previous authors have used conservation status as a guide to setting the f value (Waugh et al. 2009, Sharp et al. 2011, Richard et al. 2011, Dillingham & Fletcher 2011). In Waugh et al. (2009) and Dillingham & Fletcher (2011), the International Union for Conservation of Nature (International Union for Conservation of Nature (IUCN) 2010) threat status was used, with f values of 0.1 for "Endangered" and "Critically Endangered" species; 0.3 for "Vulnerable" and "Near Threatened" species, and 0.5 for other species. Sharp et al. (2011) recommended a similar scheme, but with f set at 0.1 for "Critically Endangered", 0.2 for "Endangered", 0.3 for "Vulnerable", 0.4 for "Near Threatened", and 0.5 for other species. This system was followed in the risk assessment by Richard et al. (2011). A value of the recovery factor may be chosen for each species, by considering what errors are plausible, and by considering the requirements on the recovery time.

4.3 Model assumptions

The population model used in this study was kept simple to ensure it was sufficiently general to be applied to all species types. A simple model also minimised the number of parameters, which was important as knowledge of demographic parameters is very limited for the majority of species. However it is recognised that the breeding system of seabirds may be more complex. For example, albatrosses take several years to form pair bonds and there is a delay in breeding after the loss of a partner. This characteristic was not included in our model, as the transition probabilities between breeding states are

only known for a minority of species (e.g., Nel et al. 2003, Ryan et al. 2007). As a consequence, the productivity of these species might have been overestimated.

Density dependence is a fundamental process for assessing the sustainability of additional mortality. Knowledge of this process is limited for seabirds, because relevant research requires detailed and long-term surveys of populations, covering a wide range of densities (Newton 1998). Consequently, a simple approach was here used to model density dependence. Positive density dependence at low densities (Allee effect; Courchamp et al. 1999) was not included, owing to the lack of knowledge about this process in seabirds. In addition, the management criterion was defined so that the long-term population size would be at half the carrying capacity and, therefore, at densities at which this positive density dependence is not expected to occur. The analysis presented here is not appropriate for populations that are close to extinction, where Allee effects may be important.

In this study, the management criterion was defined according to the carrying capacity. Knowledge of the absolute carrying capacity was not required, because the fishing-related mortality was assumed to be proportional to the population size. If the population is in fact close to the carrying capacity, however, then the adult survival may be reduced. This would result in an increased estimate of the PBR.

The calculation of the calibration factor, ρ, was made with values of the environmental stochasticity drawn so that typical populations had a c.v. of 0.1. This choice will not be generally applicable. In cases where environmental variation is causing the population to fluctuate more extremely, a lower PBR will be needed if the population is to achieve the management criterion. In this case, a lower ρ value would be appropriate.

4.4 Differences with Wade (1998)

Wade (1998) validated the PBR methodology using simulations of marine mammal populations. In his simulations, the number of annual mortalities was set equal to the PBR, which was updated at a regular interval, therefore assuming that human activities respond immediately to management. In contrast, we first calculated the maximum human-caused mortality rate that was consistent with the management criterion, then tested the performance of the PBR formula in estimating the maximum mortalities (the product of the rate and the initial population size). The PBR is not envisioned as a means to set levels of human-caused mortality, but as a tool to detect levels of fishing-related mortality that fail the management criterion. This approach is closer to current management process, which is setting priorities for the species that are the most at risk, rather than setting the level of fisheries-related mortalities for each species.

The initial model by Wade (1998) only had three demographic parameters, the population size (N), the maximum net recruitment rate (r_{max}), and the carrying capacity (K). Here, the vital rates were explicit. Annual survival for three age classes (chicks, immatures, and adults), clutch size, age at first reproduction, probability of breeding, and the intensity of density dependence were separate parameters, allowing the consequence of biases in each parameter to be examined. Moreover, the carrying capacity was implicit, as density dependence was included in the adult and chick survival, as well as in the probability of breeding. In contrast, carrying capacity was a defined parameter in the model of Wade (1998). Furthermore, in his model, Wade (1998) fixed the model parameters. For example, carrying capacity was set to 10 000 individuals throughout his study. Here, we explored a range of values for each modelled species type.

In the analysis by Wade (1998), the PBR was tested against two criteria: (1) that populations starting at the maximum net productivity level (MNPL) stayed there or above after 20 years, and (2) that populations

starting at 30% of carrying capacity recovered to at least MNPL after 100 years. In this analysis, a single criterion was used: that populations were above half the carrying capacity after 200 years. This criterion was defined probabilistically, with the initial populations being uniformly drawn from between 5% and 100% of the carrying capacity. Because of the inclusion of environmental stochasticity, the recovery time criterion set by Wade (1998) would have been difficult to meet for long-lived seabird species with a high probability. Instead, the analysis in this study focused on the long-term status of seabird populations.

5. ACKNOWLEDGMENTS

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