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Estimating the ability of birds to sustain additional human-caused mortalities using a simple decision rule and allometric relationships

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ABSTRACT

Many bird species are subject to human-caused mortality, either through direct harvest (e.g. game birds) or through incidental mortalities (e.g. fisheries-related bycatch of seabirds, impact with vehicles, wind turbines, or power lines). In order to assess the impact of additional mortalities on birds, both the number of birds killed and their ability to sustain those deaths must be estimated. Niel and Lebreton [Niel, C., Lebreton, J.-D., 2005. Using demographic invariants to detect overharvested bird populations from incomplete data. *Conservation Biology* 19, 826–835] applied a simple decision rule [Wade, P.R., 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. *Marine Mammal Science* 14, 1–37] to estimate the level of additional human-caused mortality or potential biological removal (PBR) that can be sustained for bird species given only (1) estimates of the population size, adult survival, and age at first breeding, and (2) the current population status and management goals. We provide guidelines for appropriate use of the method and case studies comparing results from this method to other approaches. Particular focus is placed on applying the method to Procellariiformes.

PBR limits may then be set without a population model and when monitoring levels are minimal, and in a computationally straightforward manner. While this approach has many advantages, there are limitations. The PBR rule was initially developed for cetaceans and pinnipeds and there have been no adaptations for the unique biology of birds which may need further consideration. Additionally, because this is a simplifying method that ignores differences in life stages, it may not be appropriate for very small populations or for those listed as ‘critically endangered’, and further work is needed for situations where mortalities have large gender or age bias.

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1. Introduction

The annual growth rate, current status, and management objectives for a species determine the level to which it can sustain additional mortalities. Among bird species, harvests or incidental mortalities come from a variety of sources, such as indigenous harvest, recreational hunting, collision with

man-made objects (vehicles, wind turbines, power lines), and bycatch in fisheries. This work was motivated by our work on fisheries bycatch of seabird species (primarily Procellariiformes such as albatrosses, shearwaters, and petrels) in New Zealand where limited demographic information is available. Typically, demographic information is limited to rough estimates of the population size, adult survival, and

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age at first breeding (Brooke, 2004). This constraint meant that a method for estimating potential biological removal from minimal information was needed.

In the marine mammal setting, Wade (1998) developed a simple rule for estimating allowable bycatch of pinnipeds and cetaceans. Potential biological removal (PBR), or the number of additional mortalities than can be sustained each year by a population, may be calculated given an estimate of the population size, the maximum annual recruitment rate (R_{\max}), and a management objective. While the rule is simple, it allows for density-dependence, stochasticity, and the potential for bias in its estimate of PBR. Among similar rules, the Wade rule performed best over a range of conditions (Milner-Gulland and Akçakaya, 2001), including different growth-fecundity combinations, suggesting that it can be used for a variety of species. However, while methods to estimate population sizes are available for a wide variety of species, R_{\max} is only observable under optimal conditions. In order to use the Wade rule for species under non-optimal conditions, R_{\max} must be estimated.

For bird species, Niel and Lebreton (2005) provide an estimate for R_{\max} given only adult survival (s) and age at first reproduction (α) under optimal conditions. In addition to being mathematically simple, this approach is relevant to the available data: while detailed knowledge of the biology of many species is limited, reasonable estimates for s and α are often either directly available or may be inferred from similar species. Niel and Lebreton (2005) apply the decision rule of Wade (1998) using point estimates for population size, s , and α , but do not explore the impact on the PBR of uncertainty in these estimates. The impact of uncertainty is important to consider, as s and α are typically estimated under non-optimal conditions and population estimates for seabirds are imprecise.

Combining the work of Wade (1998) and Niel and Lebreton (2005) allows estimation of allowable harvest levels for birds given only management objectives, an estimated population size, adult survival (s) and age at first reproduction (α). Although the PBR approach tends to be conservative (Hall and Donovan, 2001), it has the benefit of allowing decision making with minimal information, providing a quick and simple method for calculating an estimate of PBR that can be compared to an estimate of human-caused mortalities. If the estimate of such mortalities is substantially greater than the PBR, the species might be over-exploited, suggesting a need for increased monitoring, additional analysis, and possible management intervention. Conversely, if the mortality estimate is substantially below the PBR estimate, it is likely that such mortality is not a substantial force on population trends. Note that this requires all sources of human-caused mortality to be considered: in practice, some or all sources of mortality may be difficult or impossible to assess, particularly for wide-ranging species such as seabirds. In the case of a declining population, knowing that a particular source of mortality is well below the PBR estimate, could lead to focussing on alternative sources of mortality, such as ecosystem change, pollution, or disease, more quickly than might otherwise be achieved. If the PBR estimate is close to the estimate of human-caused mortality, it suggests that further information is required. Overall, use of this approach means that minimal effort can provide valuable infor-

mation for a large number of species, allowing research effort and resources to be focussed on those populations for which there is a clear need.

The primary objectives of this paper are to describe the PBR method in detail and to explore the impact of uncertainty in the estimates used to calculate the PBR. We provide three examples of its use. The first two involve the greater snow goose (*Anser caerulescens atlanticus*) and the magpie goose (*Anseranas semipalmata*), and allow us to compare the results with those from a detailed population model. The third example involves white-chinned petrel (*Procellaria aequinoctialis*), where relatively little is known about the population, and for which there appears to be high level of human-caused mortality, from bycatch in longline fisheries.

2. Methods

Potential biological removal (PBR), or the number of additional mortalities than can be sustained each year by a population, is estimated by

$$\text{PBR} = \frac{1}{2} R_{\max} N_{\min} f \quad (1)$$

where R_{\max} is the maximum annual recruitment rate, N_{\min} is a conservative estimate of population size (Wade (1998) recommended the 20th percentile) and f is a recovery factor between 0.1 and 1 (Wade, 1998; Taylor et al., 2000; Hunter and Caswell, 2005; Niel and Lebreton, 2005). This simple formula can be applied to a variety of management objectives, such as maintaining a species at or above the maximum net productivity level (MNPL; the population size at which the annual increase in population size is maximised) or minimizing time to recovery by setting different levels of f (Wade, 1998). This method provides a conservative estimate of PBR for the MNPL objective, assuming a convex ($\theta > 1$) or logistic ($\theta = 1$) density-dependent growth curve, given by

$$N_{t+1} = N_t + R_{\max} \left[1 - \left(\frac{N_t}{K} \right)^\theta \right]$$

where N is abundance, t is time, and K is the carrying capacity (Wade, 1998). While the rule is simple, it allows for density-dependence, stochasticity, and the potential for bias in its estimate of PBR, and was developed through extensive simulation.

While methods to estimate population sizes are available for a variety of species, and the recovery factor is based on a management decision, R_{\max} is only observable in optimal conditions. In order to use Eq. (1) for species in non-optimal conditions, R_{\max} must be estimated by other means. Niel and Lebreton (2005) use allometric relationships (Blueweiss et al., 1978; Allainé et al., 1987; Gaillard et al., 1989) to estimate R_{\max} in terms of adult survival (s) and age at first reproduction (α) for a variety of bird species. This key result allows a mathematically simple approach to estimating the PBR for bird species.

2.1. Estimating R_{\max}

The maximum recruitment rate (R_{\max}) and maximum annual population growth rate (λ_{\max}) are related by the equation

$R_{\max} = \lambda_{\max} - 1$. With appropriate demographic information, matrix population models can be constructed to estimate λ_{\max} (Caswell, 2001). However, for many species too little data is available to construct such matrices.

The methods of Niel and Lebreton (2005) allow estimates of a theoretical maximum annual growth rate (λ_{\max}) and the mean optimal generation length (\bar{T}_{op}) knowing only age at first reproduction (α) and adult survival (s) for bird species. This approach assumes constant fecundity and constant adult survival after age of first reproduction. Two key relationships are used in the calculation by Niel and Lebreton (2005):

$$\ln(\lambda_{\max})\bar{T}_{op} \approx 1$$

and

$$\bar{T}_{op} = \alpha + \frac{s}{\lambda_{\max} - s}$$

Combining these yields

$$\lambda_{\max} = \exp \left[\left(\alpha + \frac{s}{\lambda_{\max} - s} \right)^{-1} \right] \tag{2}$$

which can be solved using numerical methods. Alternatively, Niel and Lebreton (2005) provide a quadratic solution based on a first-order Taylor series approximation. Niel and Lebreton (2005) show for 11 bird species undergoing growth that the estimates from Eq. (2) are similar to estimates achieved from matrix approaches ($R^2 = 0.884$). These species have a variety of life history traits, including early ($\alpha = 1$) to late ($\alpha = 12$) reproduction, and low ($s = 0.73$) to high ($s = 0.987$) survival (Niel and Lebreton, 2005). Maximum growth rates for a variety of survival/age at first reproduction combinations are shown in Fig. 1.

In practice, population parameters (α, s) may not be available for all species of interest and would rarely be available for optimal conditions. If life history data for a similar species are available, it may be reasonable to use estimates from that species. Otherwise, plausible values for α and s may be reasonably estimated from data at hand, providing a plausible range for λ_{\max} .

2.2. Estimating N_{\min}

To calculate the PBR requires a conservative estimate of the population size (N_{\min}), suggested by Wade (1998) to be the

lower bound of a 60% confidence interval. That is, the PBR decision rule incorporates both the population estimate and an estimate of the uncertainty surrounding it. Depending on the species, population estimates may be characterized in several ways, such as an estimate (\hat{N}) and standard error ($\hat{\sigma}_N$), an estimate and a coefficient of variation ($CV_N = \hat{\sigma}_N/\hat{N}$), or as an upper (N_U) and lower limit (N_L) for a $(1 - \alpha)\%$ confidence interval. In some cases these may be estimated directly by the researcher, or may be available in the literature.

Wade (1998) assumed that the population estimate (\hat{N}) followed a log-normal distribution with known coefficient of variation ($CV_N = \sigma_N/N$), where the p th percentile estimate is given by

$$N_p = \hat{N} \exp \left(Z_p \sqrt{\ln(1 + CV_N^2)} \right) \tag{3}$$

where Z_p is the p th standard normal variate. For $N_{0.2}$, the lower bound of a 60% confidence interval, $p = 0.2$, and $Z_p \approx -0.84$. In practice, percentile estimates (\hat{N}_p) are based on an estimated coefficient of variation (CV_N) rather than a known one. The ratio of the two percentile estimates is

$$\frac{\hat{N}_p}{\hat{N}_q} = \exp \left(Z_p \left(\sqrt{\ln(1 + CV_N^2)} - \sqrt{\ln(1 + CV_N^2)} \right) \right)$$

In practice, this difference may be small if CV_N is reasonably close to CV_N , but can be substantial otherwise. For example, if $CV_N = 0.5$ and $CV_N = 0.4$, there is an 8% bias in $\hat{N}_{0.2}$, which increases to 21% for $CV_N = 0.25$.

In some cases, such as when decision makers must use estimates available in the literature, the only population estimates available may be upper and lower bounds of a $(1 - \alpha)$ confidence interval. In these cases, and assuming that the confidence interval is again based on a log-normal distribution

$$\hat{N} = \sqrt{N_L N_U} \tag{4}$$

and

$$CV_N = \sqrt{\exp \left(\left(\frac{\ln(N_U/N_L)}{2Z_{1-\alpha/2}} \right)^2 \right) - 1} \tag{5}$$

Eqs. (4) and (5) may then be used in Eq. (3) to estimate N_p .

A Taylor series approximation, $\ln(1 + CV_N^2) \approx CV_N^2$, may be used in Eq. (3) to estimate $N_{\min} = \hat{N}_{0.2}$ as

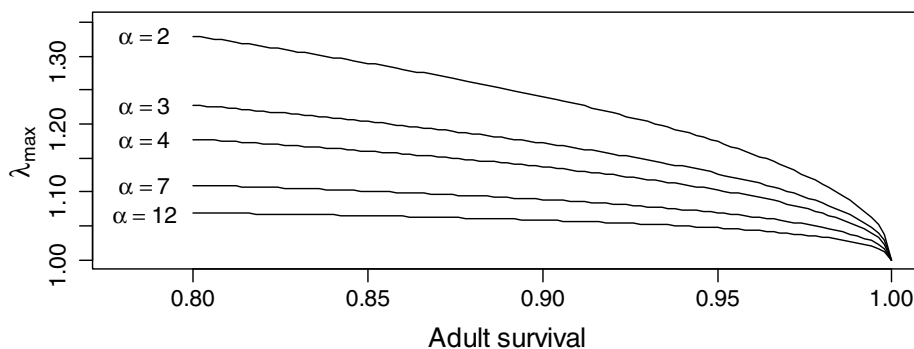


Fig. 1 – Maximum annual growth rate (λ_{\max}) as a function of age at first breeding (α) and adult survival estimated by the methods of Niel and Lebreton (2005).

$$N_{\min} = \hat{N} \exp(Z_{0.2} CV_{\hat{N}}) \quad (6)$$

This approximation is valid for $CV_{\hat{N}} < 0.6$, resulting in a 0 to –4% bias in $N_{0.2}$, and the approximation is reasonable up to $CV_{\hat{N}} = 1$ (–13% bias in $N_{0.2}$). Combining Eq. (6) with Eq. (1) yields

$$PBR = \frac{1}{2} R_{\max} f \hat{N} \exp(Z_{0.2} CV_{\hat{N}}) \quad (7)$$

2.3. Selecting f

The value selected for f can be used to implement alternative management strategies. For example, a value of 0.1 can be used to provide a minimal increase in recovery time for a depleted population, to maintain a population close to its carrying capacity, or to minimize the extinction risk for a population with limited range, while a value of 1 could be used to maintain a healthy, growing population at or above its maximum net productivity level (Wade, 1998; Taylor et al., 2000). Wade (1998) suggests a value of 0.5 for most healthy populations, as this provides protection against bias in population estimates, maximum growth rates, and mortality estimates. While this approach was designed to maintain a population at or above MNPL, a value of $1 < f < 2$ could be used to control a population at a lower level, while $f > 2N_{\min}/\hat{N}$ would be expected to reduce the population size no matter where it was in relation to carrying capacity.

The recovery factor f is selected based on a species' population status, with a value of 0.1 suggested for threatened or endangered species (Wade, 1998; Taylor et al., 2000; Niel and Lebreton, 2005). BirdLife International maintains the International Union for the Conservation of Nature and Natural Resources (IUCN) population status for birds. Birds are classified according to IUCN criteria (IUCN, 2001) as 'least concern', 'near threatened', or 'threatened'. 'Threatened' species are further classified as 'vulnerable', 'endangered', or 'critically endangered'. Without further information, it may be reasonable to set $f = 0.5$ for 'least concern' species, $f = 0.3$ for 'near threatened', and $f = 0.1$ for all threatened species. A value of $f = 1.0$ may be appropriate for 'least concern' species known to be increasing or stable.

Further, the value of f could be an important part of an adaptive management system (Williams et al., 2002). With ongoing monitoring, the value could be updated to reflect increasing knowledge of the system, with initial values set based on a variety of considerations but allowed to increase or decrease if warranted. For example, it may be reasonable to set $f = 0.3$ for a vulnerable species that had a large population and breeding range (i.e. some level of additional decline would not jeopardize the viability of the species), monitor the population, and determine if f needed to be lowered or could eventually be raised. Alternatively, it may be preferable to start with a conservative value ($f = 0.1$, say) and increase it after the species' status improved.

2.4. Harvest rates

In some cases it may be preferred to calculate an allowable harvest rate (h_a), rather than the PBR. The relationship between the allowable harvest rate and PBR is

$$h_a = \frac{PBR}{\hat{N}}$$

or, substituting into Eq. (1)

$$h_a = \frac{1}{2} R_{\max} f \frac{N_{\min}}{\hat{N}}$$

Using the estimate of N_{\min} from Eq. (6), this is re-written as

$$h_a = \frac{1}{2} R_{\max} f \exp(Z_{0.2} CV_{\hat{N}}) \quad (8)$$

The maximum harvest rate (h_{\max}) using the PBR approach, applied to a non-threatened species with an increasing population trend and with a perfect census is

$$h_{\max} = \frac{1}{2} R_{\max} \quad (9)$$

Thus, combining Eqs. (8) and (9), the ratio between the allowable harvest rate and maximum harvest rate is

$$h_a/h_{\max} = f \exp(Z_{0.2} CV_{\hat{N}})$$

That is, the allowable harvest rate is decreased from the maximum harvest rate by only two sources: the recovery factor and the variation in the population estimate.

2.5. Sensitivity of the PBR estimate

The PBR estimate depends on several factors, and changing any of them changes the estimate. In some cases, this change may be straightforward, while it is more complex in others. The impact of changes in different factors on the PBR may be examined through sensitivity or elasticity analyses (Caswell, 2001), or less formally, as done here. For example, increasing the recovery factor from $f = 0.1$ to $f = 0.5$ clearly results in a five-fold increase in the PBR, while an decrease in the CV from 50% to 49% would increase the PBR by approximately 0.4% (see Eq. (7)). Both of these results are intuitive, and are straightforward computationally. The relationships between the PBR and s and α are computationally more challenging and less intuitive.

For example, the Chatham albatross (*Thalassarche eremita*) is a critically endangered species which has an estimated survival of $s = 0.87$ (Robertson et al., 2003). However, other albatrosses typically exhibit survival rates of 0.95 or more (Brooke, 2004). It is important to understand the impact on the PBR of using $s = 0.87$ versus using a survival estimate from other species in the genus; in general, the desire should be to use a survival rate that reflects survival during optimal conditions. Similarly, it is not always clear which value to use for α . While the Niel and Lebreton model assumes constant fecundity from the age of first reproduction, this may not always be the case. For example, great cormorants (*Phalacrocorax carbo*) begin breeding at $\alpha = 2$ but fecundity and age-specific breeding success increase until age 5 (Frederiksen et al., 2001; Niel and Lebreton, 2005). It is not immediately clear which value of α is appropriate to use in Eq. (2). For example, suppose $s = 0.89$. If $\alpha = 2$ then $\lambda_{\max} = 1.25$, whereas if $\alpha = 3$ then $\lambda_{\max} = 1.18$. The PBR based on these estimates differs by over 30%. In practice, using a mid-point value for α produces similar results to modifying the population model to allow for increasing fecundity over time, low estimates of α may be reasonable if age at first breeding is density-dependent (i.e. fecundity is reduced in

early age classes) and conditions are non-optimal, and high estimates of α produce the most conservative PBR.

In a Leslie matrix approach, which many researchers are familiar with, all else being the same, higher survival would lead to greater annual growth. However, in the Niel and Lebreton method, survival is implicitly tied to fecundity and generation length. That is, birds with the highest survival rates (e.g. albatrosses) also have the lowest fecundities. The inverse relationship between fecundity and survival means that higher survival estimates are associated with lower annual growth (Fig. 1), a counterintuitive relationship for those used to matrix models. Further, λ_{\max} quickly decreases as s approaches 1, suggesting that the validity of the Niel and Lebreton method may be questionable for very high survival estimates.

From a management perspective, this means that an underestimate of survival results in an overestimate of PBR. Survival is typically estimated using capture–recapture methods which naturally incorporate emigration but not immigration (Nichols and Hines, 2002; Peery et al., 2006). This means that survival estimates tend to be negatively rather than positively biased. Further, most survival estimates are derived in non-optimal conditions. Consequently, if survival estimates are derived in non-optimal conditions or estimates have not been adjusted for possible emigration from the study area, conservative (i.e. high) survival estimates should be used to avoid over-estimation of λ_{\max} and PBR.

Consistent with expectations from a Leslie matrix approach, low values of α are associated with low annual growth. In general, the estimated value of α can be important for birds with early fecundity, especially if survival is also low (Fig. 1). For birds with delayed fecundity and high survival, such as seabirds, changes in α lead to only small changes in λ_{\max} , and mid-point values for α are usually appropriate, while high values lead to conservative estimates of λ_{\max} and PBR.

2.6. Case studies

Three species were chosen to illustrate use of the PBR approach described in this paper. Greater snow geese are a well-studied population where λ_{\max} may be estimated using census data, matrix model approaches, or the Niel and Lebreton method. Magpie geese are a common waterfowl in tropical northern Australia with a history of indigenous and recreational harvest. Sustainable harvest rates were estimated in the late 1980s using census data (Bayliss, 1989) and more recently using a population model (Brook and Whitehead, 2005b). Finally, like many Procellariiformes, the white-chinned petrel is a species for which there is limited demographic information, and which has suffered high mortality rates in fisheries; it therefore provides an application of the approach when alternative management methods are not available.

2.7. Greater snow geese

Greater snow geese are an abundant and widespread North American goose whose population was reduced to less than 10,000 birds in the early 1900s (Menu et al., 2002). Protection measures allowed the population to rebound to 100,000 birds

by 1970, and nearly 750,000 birds by 1998 (Menu et al., 2002). After adjusting for known harvest rates, they are a good example of a species that is growing at near optimal rates.

There is now concern about overabundance, and research is focussed on finding a minimal harvest rate (h_c) that would control the population (Gauthier and Brault, 1998; Menu et al., 2002; Gauthier and Lebreton, 2004). They are well enough studied to allow population models (Gauthier and Brault, 1998; Gauthier et al., 2001; Gauthier and Lebreton, 2004) to be constructed. This, combined with accurate census data, makes this species a good one for which to compare different approaches to estimating harvest rates necessary to control the population. Available data includes census data and resulting growth rates, and harvest and/or survival rates for the periods 1970–1974, 1975–1983, and 1984–1998, corresponding to high growth/low harvest, low growth/high harvest, and moderate growth/moderate harvest periods, respectively.

Niel and Lebreton (2005) compared a matrix model estimate of $\lambda_{\max} \approx 1.167$ from Gauthier and Brault (1998), with a point estimate of $\lambda_{\max} \approx 1.21$ (Eq. (2)), using $s = 0.83$ and $\alpha = 3$. This survival rate includes hunting mortality; both approaches may be improved by estimating survival in the absence of hunting (natural survival, s_0). For the period 1990–1998, Gauthier et al. (2001) estimated this as $\hat{s}_0 = 0.91$ compared to an estimate from Gauthier and Brault (1998) of $\hat{s}_0 = 0.88$. The higher estimate (all else the same) increases the matrix model estimate to $\lambda_{\max} \approx 1.257$, and decreases the estimate to $\lambda_{\max} \approx 1.164$ (Eq. (2)); both approaches are sensitive to the estimate of s but in opposite directions. A minimum harvest rate of $h_c = 10.5\%$ for adults was estimated to result in a stable or declining population (Gauthier and Lebreton, 2004).

Growth rates from census data and harvest rate estimates (Menu et al., 2002) from the three periods were used to provide a census-based estimate of λ_{\max} . Since most birds that were harvested would have otherwise survived and had offspring at normal rates (i.e. assuming additive mortality, an assumption supported by Gauthier et al., 2001), the observed growth rate is approximately $\lambda \approx \lambda_{\max}(1 - h)$, or $\lambda_{\max} \approx \lambda/(1 - h)$. Hence, potential growth rates for each time period ($\lambda_{\max,p}$) were estimated as the ratio of the observed growth (λ_p) and the complement of the harvest rates. Adult harvest rates for each period (h_p) were used, as the population is most sensitive to these, and juvenile survival rates were low (although it is important to note that young geese are disproportionately harvested; Menu et al., 2002; Gauthier and Lebreton, 2004). Hunter and Caswell (2005) provide some discussion on this topic, although for purposes of illustration differential harvest rates between age classes are ignored. For each time period, the period-specific maximum growth rate was then estimated as

$$\hat{\lambda}_{\max,p} = \frac{\hat{\lambda}_p}{1 - \hat{h}_p}$$

Assuming independence between λ_p and h_p , and using the delta method (Rice, 1995)

$$\hat{\sigma}_{\lambda_{\max,p}} \approx \frac{1}{1 - \hat{h}_p} \sqrt{\hat{\sigma}_{\lambda_p}^2 + \hat{\sigma}_{h_p}^2 \left(\frac{\hat{\lambda}_p}{1 - \hat{h}_p} \right)^2}$$

In order to weight the growth rate in each year equally, λ_{\max} was estimated as

$$\hat{\lambda}_{\max} = \sum_{p=1}^3 w_p \hat{\lambda}_{\max,p} \quad \text{and} \quad \hat{\sigma}_{\lambda_{\max}}^2 = \sum_{p=1}^3 w_p^2 \hat{\sigma}_{\lambda_{\max,p}}^2$$

where $w_p = \#\{\text{years in period}\} / \#\{\text{all years}\}$. A plausible range was considered to be $\hat{\lambda}_{\max} \pm 2\hat{\sigma}_{\lambda_{\max}}$; the use of the term confidence interval is avoided due to uncertainty in the shapes of the distributions involved and to the simplifications and approximations used. From this, Eq. (9) was used to estimate h_{\max} as a proxy for h_c . However, the PBR method is designed to keep a population at or above MNPL; if the desired population level is below this value then the required harvest rate may be greater than h_{\max} (e.g. $f > 1$). An empirical estimate is also available, noting that $\lambda \approx \lambda_{\max}(1-h) \Rightarrow \hat{h}_c = 1 - 1/\hat{\lambda}_{\max}$ by setting $\lambda = 1$ with approximate standard error $\hat{\sigma}_{h_c} \approx \hat{\sigma}_{\lambda_{\max}} / \hat{\lambda}_{\max}^2$.

In addition to the growth and harvest rates used above, Menu et al. (2002) provided independent estimates of adult survival for the periods 1970–1974 and 1984–1998. This allows the uncertainty in adult survival and age at first breeding, and an adjustment for harvest rates, to be incorporated into the estimate of λ_{\max} from Eq. (2), generating a plausible range. Once again assuming that most harvested birds would have otherwise survived, potential or natural survival for each period ($\hat{s}_{0,p}$) is approximated as the ratio of adult survival for the period (\hat{s}_p) and the complement of the adult harvest, or

$$\hat{s}_{0,p} = \frac{\hat{s}_p}{1 - \hat{h}_p}$$

From the delta method

$$\hat{\sigma}_{s_{0,p}} \approx \frac{1}{1 - \hat{h}_p} \sqrt{\hat{\sigma}_{s_p}^2 + \hat{\sigma}_{h_p}^2 \left(\frac{\hat{s}_p}{1 - \hat{h}_p} \right)^2}$$

Natural mortality was then estimated in an analogous manner to λ_{\max} , with weights based on the period length. Finally, while some birds begin breeding by age two, breeding propensity increased from 0.35 at age 2 to 0.77 and 0.85 at ages 3 and 4, respectively (Gauthier and Braut, 1998). Values from $\alpha = 2$ to $\alpha = 4$ are reasonable for this species, with the best estimate being $\alpha = 3$. Survival and breeding estimates were used in Eqs. (2) and (8) to provide plausible ranges for λ_{\max} and h_{\max} , where plausible ranges were the middle 95% of 10,000 samples, each generated by sampling from $\alpha \in \{2, 3, 4\}$ with probability $p_a = \{0.25, 0.50, 0.25\}$ and $s_0 \sim N(\hat{s}_0, \hat{\sigma}_{s_0})$. Finally, estimates of λ_{\max} and the harvest rate necessary to control the population from the three approaches were compared.

2.8. Magpie geese

Magpie geese are a common waterfowl in tropical northern Australia, currently harvested at a rate of up to 18% of the population, and it is unclear if this rate is sustainable (Brook and Whitehead, 2005a). They number approximately 3.5 million (Brook and Whitehead, 2005a), with a reasonable lower bound of 2 million (Bayliss and Yeomans, 1990; Brook and Whitehead, 2005b). Between 130,000 and 360,000 birds are harvested annually (Brook and Whitehead, 2005a). The primary source of harvest is indigenous (100,000–290,000 annu-

ally), with another 30,000–70,000 per year harvested recreationally (Brook and Whitehead, 2005a). Thus, current harvest rates are likely between 4% and 10%, but may be as high as 18%.

Bayliss (1989) and Brook and Whitehead (2005b) estimated the maximum annual rate of population growth in order to estimate allowable annual harvest rates. The maximum annual rate of population growth was estimated by Bayliss (1989) using aerial survey counts at $\lambda_{\max} = 2.18$ (i.e. a potential 118% annual population growth at low densities), with an allowable harvest rate of approximately 30% per annum. The annual harvest appears to be well below the sustainable harvest rate calculated by Bayliss (1989).

Brook and Whitehead (2005b) used matrix methods to estimate $\lambda_{\max} = 1.18$, with an extreme upper bound of $\lambda_{\max} = 1.65$ and a more realistic upper bound of $\lambda_{\max} = 1.32$. For these methods, reasonable assumptions lead to an annual sustainable harvest rate of 5–14% with a best estimate of 8.5% (Brook and Whitehead, 2005b), far lower than the 30% estimated by Bayliss (1989). Thus, their method suggests that current harvest rates may be too high.

Using the PBR approach, we only need estimates of age at first breeding, adult survival, conservation status, and population size to estimate λ_{\max} , h_a , and the PBR. Consistent with the values used by Brook and Whitehead (2005b), α was set between 2 and 3 years, with an assumed minimum adult survival rate of 0.85, a best estimate of 0.93, and an assumed maximum of 0.95. The best population estimate of 3.5 million, with a lower bound of 2 million, was used to estimate N_{\min} (Eqs. (4)–(6)). As the current population trend is unknown, a value of $f = 0.5$ is suggested by Wade (1998). In practice, the choice of f should incorporate impacts on stakeholders, such as impacts from lower harvest limits, along with conservation goals, and could also be influenced by the level of monitoring. While less information is available for magpie geese than for greater snow geese, this still allows plausible ranges for λ_{\max} , h_a , h_{\max} , and PBR to be calculated.

2.9. White-chinned petrel

Seabirds, such as the white-chinned petrel, have low fecundity and delayed maturity, making them vulnerable to any reduction in adult survival. Fisheries bycatch (and other related mortalities) are currently estimated to kill hundreds of thousands of seabirds each year (Baker et al., 2007), and there is general concern about the impact of bycatch and other threats (see Baker et al., 2002 for a good review of threats to Procellariiformes). White-chinned petrels appear to be undergoing a population decline (Berrow et al., 2000), are commonly caught in longline fisheries, and the species is listed as *vulnerable* (BirdLife International, 2007). During 1997 and 1998, between 80,000 and 200,000 seabirds were killed in the unregulated Patagonian toothfish fishery, of which approximately 60% were white-chinned petrels (SC-CALMR, 1998). They are the most commonly caught seabird species in the Southern Ocean (Weimerskirch et al., 1999). Further, bycatch in the Patagonian toothfish fishery was heavily male-skewed (>80%), with nearly all birds killed in adult plumage (Ryan and Boix-Hinzen, 1999; Nel et al., 2002). They may also be affected by future changes in marine habitat in the southern oceans (Croxall, 2004).

There are approximately 2.5 million breeding pairs of white-chinned petrels worldwide, and perhaps 7 million birds total (Brooke, 2004). These estimates are imprecise, so $CV_N = 0.5$ was assumed. Birds begin breeding around $\alpha = 6.5$ (Schreiber and Burger, 2001). One published survival estimate ($s = 0.79$; Schreiber and Burger, 2001) is clearly wrong: it apparently comes from the misapplication of $s = 0.79 + 0.019 \ln x$ where x is weight in grams (Croxall and Gaston, 1988). Based on a weight of 1350 g (Brooke, 2004), correct application of this equation suggests $\hat{s} = 0.93$ although the predictive power of the equation was only $R^2 = 0.27$ (Croxall and Gaston, 1988). For the white-chinned petrel's sister species, the spectacled petrel (*Procellaria conspicillata*), Ryan et al. (2006) suggested that plausible levels of adult survival range from 0.94 to 0.98, based on other petrels. Brooke (2004) provides estimates for related species ranging from 0.92 to 0.94. We set $\hat{s} = 0.93$ and $\hat{\alpha} = 6.5$, and considered s between 0.90 and 0.97 and α between 6 and 7 to represent a plausible range.

Given the population decline, IUCN status, and age and gender bias in mortalities, a reasonable value of f is 0.1. However, the large population size and number of breeding colonies provide a buffer against any immediate threat to the population viability, so a less conservative value of $f = 0.3$ may be acceptable if combined with adequate monitoring and a willingness to modify the value based on the monitoring. Because of the bias in gender and age in bycatch estimates, a modified PBR estimate was also estimated based on the number of breeding males rather than the total population. This is, to some extent, an ad hoc approach, and suggests future effort may be needed in this area. Finally, we note that managing a species that is vulnerable to bycatch from a variety of fisheries is a daunting task, both operationally and politically. Bycatch estimates are subject to deficiencies such as missing data, misidentification, bird loss prior to observation, and lack of standardisation (Uhlmann et al., 2005; Miller and Skalski, 2006). In this context, the PBR estimate is essentially an assessment tool to determine if estimated or plausible bycatch levels may have a detrimental effect, rather than a management tool for setting bycatch goals.

3. Results

For species such as large waterfowl or seabirds with delayed fecundity and moderate to high survival ($\alpha \geq 3$; $s \geq 0.8$), the maximum annual growth rate is less than 1.25 (Fig. 1). For large waterfowl such as geese, λ_{\max} may be near 1.2 (see examples in Niel and Lebreton, 2005), while for seabird species such as Procellariiformes, λ_{\max} is commonly less than

1.1, indicating that, even under optimal conditions, these populations can not grow faster than 7% (albatrosses), 10% (petrels, shearwaters), or 20% (large waterfowl) in 1 year. This limits their ability to sustain high levels of additional mortality and their ability to quickly recover from depletion, most especially for species such as albatrosses. For seabirds such as albatrosses and petrels, especially for populations that are threatened or depleted, the maximum harvest rate may need to be 0.5% or less in order to minimize recovery time or maintain a population close to carrying capacity. For species such as greater snow geese where the population size has created problems, harvest levels equal to or greater than h_{\max} may be required to control growth; for large waterfowl this is on the order of 10%.

3.1. Greater snow geese

Maximum growth rates (estimate \pm SE) using Eqs. (2) and (8) for greater snow geese were estimated from the census and harvest data for the 1970–1974 (1.190 ± 0.032), 1975–1983 (1.136 ± 0.016), and 1984–1998 (1.165 ± 0.011) periods, which combined to provide a census-based estimate of $\hat{\lambda}_{\max} = 1.160 \pm 0.009$. A minimal harvest rate necessary to control the population was estimated using Eq. (9) (Table 1). Empirical estimates (\pm SE) from the census-harvest data suggested $\hat{h}_c = 0.138 \pm 0.007$ for the entire time period, or $\hat{h}_c = 0.119 \pm 0.013$ for the 1975–1983 period, when high harvest rates resulted in low growth. Similarly, natural survival estimates (\pm SE) for 1970–1974 (0.869 ± 0.045) and 1984–1998 (0.851 ± 0.047) were combined to estimate natural survival (0.856 ± 0.037). Incorporating uncertainty in survival rates, together with sampling from plausible values of α , allowed uncertainty in the Niel and Lebreton (2005) estimate of λ_{\max} and the PBR estimate of h_{\max} (Eqs. (2) and (8)) to be quantified. The census-harvest estimates (CH), these estimates (NL), and the matrix model estimates (MM) from Gauthier and Lebreton (2004) are summarized in Table 1.

All of the growth and harvest estimates fall in the same general range. When growth rates are the same, the matrix model and empirical census-based estimates for h_c suggest that a somewhat higher harvest rate is necessary to maintain or reduce the population than by using $\hat{h}_c = h_{\max}$. This could be a result of inherent conservatism in the PBR approach or due to the desired population level being below the level which would be maintained by h_{\max} . Finally, bounds on λ_{\max} and h_c are largest when uncertainty is incorporated into Eqs. (2) and (8). This is quite reasonable, as these estimates are based on minimal information compared to the more sophisticated approaches available.

Table 1 – Maximum growth rate (λ_{\max}) and the harvest rate (h_c) required to prevent population growth in greater snow geese using matrix models (MM), and census-harvest (CH) and Niel and Lebreton (2005) (NL) growth estimates combined with the PBR harvest rate estimate

Method	λ_{\max}	Plausible range	h_c (%)	Plausible range
MM	1.167	na	10.5	na
CH	1.160	(1.148, 1.178)	8.0	(7.4%, 8.9%)
NL	1.200	(1.134, 1.323)	10.0	(6.7%, 16.2%)

3.2. Magpie geese

Assuming age at first reproduction between 2 and 3 years and survival ranging from 0.85 to 0.95, the plausible range for λ_{\max} is 1.13–1.29, with a best estimate of $\lambda_{\max} = 1.17$. Thus, if the population were known exactly and known to be increasing, it would be reasonable to set the harvest rate at $h_{\max} = 8.5\%$, ranging from $h_{\max} = 6.5\%$ to $h_{\max} = 14.5\%$, similar to the range provided by Brook and Whitehead (2005b). However, when we protect against potential bias and include uncertainty in the population estimate, the PBR method suggests a lower harvest rate. With a population estimate of 3.5 million, a lower bound 2 million, and assuming the lower bound comes from a 95% CI, N_{\min} is approximately 2.8 million (Eqs. (4)–(6)). Combining this with a ‘best’ population estimate of 3.5 million, and setting $f = 0.5$ (as suggested by Wade (1998) when the population trend is unknown) leads to a harvest rate from Eq. (8) of $h_a = 3.3\%$ (Eq. (7)), ranging from $h_a = 2.6\%$ to $h_a = 5.7\%$. Thus, while initial harvest rate estimates are similar to Brook and Whitehead (2005a,b), once variability in population estimates, protection against potential bias in population estimates or harvest levels, and the unknown trend are considered, PBR harvest rates are reduced by more than 50%. A less conservative estimate may be reasonable if there is ongoing monitoring of the species (i.e. $f = 1.0$ leads to $h_a = 6.6\%$).

Given current knowledge of the population, total harvests under 120,000 birds would be recommended by the PBR method. Thus, the current harvest of at least 130,000 birds is higher than would be suggested without greater knowledge of the population, and is potentially even occurring at a rate greater than h_{\max} . If the population were found to be increasing, the harvest could be increased to 230,000 birds. Given that current harvests are at, near, or above the PBR levels, the customized approach to the specific conditions of the species and the associated harvest methods and pressures, such as that undertaken by Brook and Whitehead (2005a), was very valuable. However, the PBR approach is again validated as giving results similar to those from a more sophisticated analysis, and, in other contexts, could have been used to suggest that a more sophisticated analysis was needed.

3.3. White-chinned petrels

The approximately 7 million white-chinned petrels (Brooke, 2004), and the assumption that $CV_N = 0.5$, leads to $N_{\min} = 4.6$ million. Assuming $\alpha = 6.5$ and $s = 0.93$, $\lambda_{\max} \approx 1.08$, with a plausible range from 1.06 to 1.10. This range is consistent with other petrels and shearwaters, while albatross populations may grow 4–7% annually in optimal conditions. Using $\lambda_{\max} \approx 1.08$ and $f = 0.1$, the mortality rate for white-chinned petrels should be below $h_a = 0.27\%$ and annual human-caused mortalities (plausible range) should be limited to 19,000 birds (14,000–24,000 birds); a less conservative approach, with $f = 0.3$, would allow mortalities up to 57,000 birds (43,000–71,000 birds). Annual mortality estimates from the 1990s Patagonian toothfish fishery were well above the PBR with $f = 0.1$ and were possibly above the PBR with $f = 0.3$.

Further, when considering the PBR estimate based only on the 2.5 million breeding males (adult males constitute

approximately 80% of the bycatch), mortality limits drop to 6800 ($f = 0.1$) and 20,000 ($f = 0.3$). When considering the gender and age bias in bycatch, it appears that annual mortalities were past those suggested by $f = 0.3$. While it is difficult to assess the impact on the population from these levels of mortality, it is clear that bycatch from just one fishery had the potential to cause harm to the population, suggesting that concerns about bycatch levels are justified.

4. Discussion

The PBR method may be used both to set harvest or bycatch limits and to compare current human-caused mortalities with the PBR estimates. This can allow quick detection of potentially over-exploited species, as well as detection of species where current harvest rates are likely to be sustainable. If human-caused mortality rates from all sources total less than h_a , then they should not be the primary cause for any concern. If a population is known to be in decline in these circumstances, other causes should be investigated. For mortality rates between h_a and h_{\max} , human-caused mortality may be occurring at an unsustainable rate, further investigation is warranted, improved knowledge of the population is desirable, and mitigation measures should be considered. Finally, if mortality rates are greater than h_{\max} , it is likely that human-caused mortalities are occurring at a rate detrimental to the species and should be reduced.

Of course, estimating the number of human-caused mortalities is a daunting task in its own right, and it is important that all substantial sources of mortality are included. For example, in the white-chinned petrel example only direct mortalities from a single fishery were considered, and these estimates were imprecise. Estimating bycatch levels for even common species vulnerable to multiple fisheries is challenging and typically requires a large number of assumptions; for rare species these problems are magnified (Uhlmann et al., 2005). In addition to other sources of bycatch mortality, there may be indirect mortalities that occur through competition for food stocks with fisheries or through marine habitat change due to global climate change. Some species may be impacted by collisions with man-made objects, such as wind turbines (Everaert and Stienen, 2007), power lines (Bevanger, 1998), or motor vehicles (Forman and Alexander, 1998). Similarly, many waterfowl species are subject to direct harvest but may also be vulnerable to human-caused habitat loss or degradation. In contexts where only one source of human-caused mortality is considered, the interpretation of the PBR changes. In these cases, PBR estimates above single-source mortality levels may suggest that those mortality levels are sustainable if there were no other human-caused mortalities. Hence, that information coupled with a declining population may suggest that effort be directed towards evaluating other sources of human-caused mortality.

The PBR mortality limits tend to be precautionary as little is assumed about the population structure, a conservative population estimate is used, and the potential for biased population estimates is generally included by setting $f < 1$. The selection of f is a management decision and should be done

with care, balancing conservation goals, stakeholder desires, and the ability to monitor the population. Coupled with conservative estimates for survival and age at first reproduction, estimates may become overly conservative. However, this approach remains a powerful tool for making management decisions when minimal information is available and for directing resources towards species of concern. In general it is limited by the requirement of an estimate of R_{\max} which may be unavailable for some species. When combined with maximum growth rate estimates from Niel and Lebreton (2005), the PBR approach may be applied to bird species with appropriate choices for α and s . With independent estimates for the components of Eq. (1), high values of α and s are conservative, and may be chosen from studies of the species of interest or of similar species. For some species the estimates of α , s , and N may not be independent. In these cases, high values of α and s may no longer be conservative. For example, if α is also used to estimate the number of unseen juvenile age classes (as may be reasonable for seabirds), λ_{\max} is still negatively related to α , but N would be positively related to α ; the overall effect on the PBR is unclear.

Many bird species – especially seabirds – have similar life histories to pinnipeds and cetaceans, characterized by long life, delayed maturity, and low fecundity. Because of this, the simulation work performed by Wade (1998) in developing the rule for cetaceans and pinnipeds is especially relevant for seabirds, where maximum growth rates for species of particular interest to New Zealand managers are in the 4–10% range. However, gender and age bias in bycatch rates suggest that extensions to this method, beyond the ad hoc approach used in the case study on white-chinned petrels, need to be developed. While there are limitations to this approach, it appears to provide similar answers to more sophisticated analyses, and is a reasonable approach when there is minimal information available. The results of Milner-Gulland and Akçakaya (2001) suggest that the rule could be applied to a variety of other bird species as well, such as moderately-lived gamebirds and waterfowl, but it may be less appropriate for short-lived species such as songbirds. The PBR method also ignores differences in life stages and gender. If there is a large age or gender bias in mortalities, and no adjustments to the method are made, the results may be misleading. By itself, the method is not appropriate for very small populations or for those listed as ‘critically endangered’. That is, it should not replace other impact analyses (for example, see Inchausti and Weimerskirch, 2001, or Zador et al., 2008), but could be still be useful as an additional tool for researchers studying these populations.

More complex population models, such as matrix models, can perform well when relevant population parameters are known. Their complexity may allow a level of realism beyond that possible through the simplified model used to estimate λ_{\max} and the simple PBR decision rule. In the case studies where results from different methods were compared, more sophisticated methods yielded more precise results. Additionally, when assumptions can be made regarding missing population parameters, matrix approaches are still valuable, both in general population modelling and as a method to estimate λ_{\max} . However, the PBR method, combined with the Niel and Lebreton method for estimating λ_{\max} , requires very little information in order to arrive at a decision and is easy to cal-

culate. Finally, the PBR method, having undergone considerable simulation study, is quite robust to estimation errors (Wade, 1998; Milner-Gulland and Akçakaya, 2001).

The PBR method can be used whatever estimate of λ_{\max} is available, whether it is from Eq. (2), a matrix approach, or from census data. However, direct estimation of λ_{\max} via matrix or census methods requires a quickly growing population, where density-dependence is unlikely to be a factor. Even in cases where this occurs, estimation via matrix methods requires more information than the Niel and Lebreton method, and estimation via census trends requires long time-series. Alternative methods, such as placing reasonable bounds on unknown parameters in matrix models, may lead to imprecise estimates of λ_{\max} , due to the number of parameters that need to be estimated.

The Niel and Lebreton (2005) estimate of λ_{\max} combined with the PBR approach is a valuable tool for management of bird species. It may be used as an initial tool to direct resources and research effort towards species where more information is needed to assess whether mortality levels are sustainable. For species where minimal information is available such as seabirds, it provides a way to assess mortality levels or harvest rates.

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