Population modelling of albatrosses and petrels with minimal demographic information

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Abstract

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There are hundreds of thousands of fisheries-related mortalities of seabirds each year. Population trends for these species are highly influenced by changes in adult survival, their maximum growth rates are low, and little additional mortality can have a large impact on the population. As a result, many albatrosses and petrels are at risk of extinction, but limited demographic data makes it difficult to quantify the risk for many species. The goal of this research is to use population modelling tools to assess potential impacts with minimal data. In particular, the question of how much additional mortality a population can sustain is addressed when there is only knowledge of the adult survival rate, age at first breeding, and the number of breeding pairs.

In this thesis, a simple decision rule designed for marine mammals is applied to albatrosses and petrels. In order to use this rule, adult survival, age at first breeding, a minimum estimate of the population size, and the maximum growth rate of the population are needed. While estimation of adult survival is well developed, work was required to calculate the other values from available data. A simple population model was developed to extrapolate from the number of breeding pairs to the total population size (given survival and age at first breeding); the effect of variable fecundity rates on the calculation of generation time and the maximum growth rate of a population was examined, relative to an estimate that only requires survival and age at first breeding; and a method for estimating the age at first breeding using capture-recapture data was suggested that accounts for study duration and emigration, in addition to capture probability.

This work can help managers make better informed decisions when little is known about a population. For example, around 5,800 pairs of Gibson's albatrosses (*Diomedea gibsoni*) breed each year. Based on the work presented in this thesis, they may be able to sustain 1,000 – 1,200 additional mortalities per year. However, given concern about their conservation status, a mortality level below 100 – 120 is desired, and any mortality beyond that level suggests a need for more intensive management.

PREFACE

This work was financially supported by the New Zealand Ministry of Fisheries (contract ENV2004/05) and the Beverly Fund of the University of Otago. A large proportion of Chapter 2 has appeared in the journal Biological Conservation (2008; 141:1783-1792.) authored by myself and David Fletcher; David suggested the topic, provided comments, and proposed revisions, while I was the primary author. We are grateful to two anonymous reviewers, whose kind suggestions improved the manuscript, and to Prof. Navjot Sodhi for managing the editorial process.

In Chapter 5, the analysis of Gibson's albatrosses would not have been possible without the data collected and provided by G. Elliott and K. Walker, and I am grateful to them for providing it to me, and to providing me with comments on the chapter. This chapter extends previous work performed by myself and Darryl MacKenzie in Fletcher et al. 2008. In that work, I performed analyses for juveniles and pre-breeders, while Darryl MacKenzie analysed adult Gibson's albatrosses.

Appendix A is an updated and edited version of Appendix A.5 in Fletcher et al. 2008. The relevant portion of the original report was prepared by Peter Dillingham with input from David Fletcher. The current version has incorporated additional methodology (primarily methods described in Chapter 3) developed for this thesis.

Finally, comments from the three reviewers for this thesis have improved it, and I am grateful for the time and effort they put into the examination process.

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Most of all, I would like to thank Christina, Hannah, and Niamh, and my parents, Jean and Edward, and my brothers, Eric, Tim, and Colin, for all of their love and support through the years.

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Chapter 1. Introduction to population modelling of albatrosses and petrels with minimal demographic information

It was only that and light was all it needed and a certain cleanness and order.

-Ernest Hemingway, *A Clean, Well-lighted Place* (1933)

Albatrosses and petrels (the Procellariiformes) are naturally long-lived birds, killed on land and at sea by sources of anthropogenic origin, likely at rates beyond those they can sustain. The New Zealand region is home to the breeding colonies for over forty Procellariiform species, many of which are threatened (BirdLife International 2009), and understanding their population structure and reaction to changes in survival or other demographic parameters is important to their management. There is a dearth of data for most of these species for many demographic parameters (Brooke 2004a), and the inaccessibility of colonies make many species difficult and costly to study.

Procellariiform populations are sensitive to changes in adult survival (Crespin et al. 2006), which means that their ability to sustain mortalities beyond natural mortality is limited (Chapter 2). While many species are thought to be in decline (Gales 1998), definitive population trends are lacking for most species (Baker et al. 2002), and population estimates are based on rule-of-thumb multipliers from estimates of the number of breeding pairs (Gales 1998, Taylor 2000, Brooke 2004a, Brooke 2004b). This means that there is a need to manage the species using minimal demographic data, and developing a way to assess the impacts or likely impacts from human activities. In short, there are two important questions that need to be addressed: (1) how many additional deaths beyond natural mortality can each species sustain, and (2) how many deaths beyond natural mortality are occurring? This thesis addresses the first question using a population modelling approach, particularly in the context of limited data.

1.1 Relevant biology of New Zealand Procellariiformes

Procellariiformes are colonial, often building their colonies in difficult to access locations, such as steep offshore islands in the sub-Antarctic (Schreiber and Burger 2002). The order is divided into four families: the albatrosses (Diomedeidae), the petrels (Procellariidae), the diving petrels (Pelecanoididae), and the storm petrels (Hydrobatidae); in this thesis, the three petrel families are generically referred to as petrels, with emphasis placed on species in family Procellariidae. Many species are limited to small populations with very few colonies in a small geographic area, while a few species such as sooty shearwater (*Puffinus griseus*, also known as tītī in New Zealand) and white-chinned petrels (*Procellaria aequinoctialis*) are common and have numerous colonies (Brooke 2004a). They are characterized by high survival rates and delayed and low fecundity, with larger birds such as albatrosses having the highest survival rates (Appendix A).

Nearly all species lay a maximum of one egg per year, and some albatross species (such as those in *Diomedea*) skip a year of breeding after successfully rearing a chick. Fledged chicks spend a number of years at sea before returning to a colony as pre-breeders. After a prospecting period, birds form strong pair-bonds, and both members of the pair raise young birds. Pairs show fidelity to breeding sites from year to year.

Breeding success (the probability that a laid egg will result in a fledged chick) is typically high, although more variable than survival, and is subject to environmental conditions (Chastel et al. 1995, Jenouvrier et al. 2005). Greater detail on the biology of Procellariiformes is available from a variety of sources: Brooke (2004a) has detailed descriptions of individual species, and Schreiber and Burger (2002) provide a good general introduction to seabird biology.

In some ways, Procellariiformes are good candidates for building population models, while there are also difficulties. Strong site fidelity for most species – especially albatrosses – means that they are good candidates for capture-recapture studies, as repeat observations on the breeding population may be achieved. This allows precise estimation of survival rates for adult breeders for many species, and can also be used to estimate the age at first breeding by banding chicks and observing them returning (e.g. Jenouvrier et al. 2005, Crespin et al. 2006). For burrowing species (*Puffinus*), field methodology becomes more complex (e.g. Imber et al. 2003, Clucas et al. 2008). In addition, access to many colonies is costly, and accurate assessment, especially of age at first breeding, may take many years of field work.

Demographic parameters for juveniles are difficult to estimate as they are not present in the study area. Survival estimates for juveniles can only be based on birds banded as chicks, and naturally incorporate emigration as well as mortality. Moreover, they can not be assessed for a number of years, when birds begin returning to the colony. Further, birds return to the colony and begin breeding at different ages (Jenouvrier et al. 2008), further complicating estimation. In a typical situation, where a small area of a colony is studied, annual survival estimates for juvenile birds are of limited use (unless emigration can otherwise be estimated). Even in the best cases (emigration known), they would represent average survival prior to return, or a model-based analog.

Population estimates ($\hat{N}$) for most seabird species are imprecise (Baker et al. 2002, Brooke 2004a). Because non-breeding birds are difficult to observe at colonies (Baker et al. 2002), census data is only available for the number of breeding pairs (or a proxy, such as the number of nests). Further, for many species, there has been no census for a number of years (Taylor 2000, Brooke 2004a). Total population estimates are based on the estimated number of breeding pairs times a rule-of-thumb multiplier (Gales 1998, Taylor 2000, Brooke 2004a, Brooke 2004b). Thus, the number of breeding pairs is used as an index of abundance. However, because even mature birds do not necessarily breed every year and a variety of factors may influence the probability of breeding (Chastel et al. 1995, Cam et al. 1998, Jenouvrier et al. 2005), short-term trends in the breeding population may not be indicative of trends in the general population, while, longer-term, the index is more useful but may be non-linear. Importantly, while it is known that population estimates derived from the number of breeding pairs are imprecise, there appears to be no information available on the level of imprecision. In Chapter 3, an improved multiplier based on a simple population model is introduced, and uncertainty around the multiplier is estimated.

The challenge of this thesis, and the challenge presented to managers, is to make calculations when the available data is limited relative to biological understanding. In some cases, data is not available to make meaningful estimates of important population parameters. In other cases, parameters of interest can not be separately identified from other parameters. One example is the problem of separating survival from emigration, where many survival estimates are actually estimates of local survival, a product of survival and not emigrating. In this case, the only way to estimate survival is to make an assumption about its relationship with emigration. The approach adopted for this work is to determine required information, and, where required, to make pragmatic assumptions allowing calculations to be made from known information.

1.2 Status of New Zealand Procellariiformes

The typical species in the New Zealand region has between 1,000 and 100,000 breeding pairs, and breeds at a limited number of locations on a few offshore islands (Gales 1998, Brooke 2004a). Due to the limited amount of census data for most species, it is difficult to know if the population is increasing or decreasing, although some species are thought to be in decline (Appendix A, BirdLife International 2009). The status of 22 individual species or sub-species of Procellariiformes deemed by the New Zealand Ministry of Fisheries to be vulnerable to fishing (Fletcher et al. 2008) and breeding in the New Zealand region is given in Appendix A.

Figure 1.1. Antipodean albatross (*Diomedea antipodensis*) lunging for a bait discard.

It is important to develop methods for assessing the status of Procellariiformes that use data that is likely to be available or reasonably inferred from similar species. In the case of New Zealand Procellariiformes, the available data is limited for most species. This necessarily leads to use of population models that simplify reality. While simple models run the risk of missing key factors, some level of simplification may have little effect on estimates of important parameters (Yearsley and Fletcher 2002). For many species, estimates of adult survival, age at first breeding, and the number of breeding pairs are available. The work presented in this thesis is motivated by limitations in data, and methods are developed with those restrictions in mind.

1.3 Threats to New Zealand Procellariiformes

There are a variety of human-caused threats to Procellariiformes in the New Zealand region and worldwide. Seabirds are attracted to fishing vessels (Figure 1.1; Barton 1979, Yorio and Caille 1999), and there have been high levels of mortalities associated with numerous commercial fisheries (Weimerskirch and Jouventin 1987, Brothers 1991, Weimerskirch et al. 1997, Gales 1998, Gales et al. 1998, Ryan and Boix-Hinzen 1999, Sagar et al. 2000, Inchausti and Weimerskirch 2001, Tuck et al. 2001, Baker et al. 2002, Nel et al. 2002, Ryan et al. 2002, Lewison and Crowder 2003, Baker et al. 2007, Croxall 2008, Moore and Žydelis 2008, Ryan and Watkins 2008, Zador et al. 2008). While it is difficult to estimate fisheries related mortalities accurately (Uhlmann et al. 2005, Miller and Skalski 2006), and mitigation measures have drastically reduced bycatch rates in some fisheries (SC-CAMLR 2006), it is thought that hundreds of thousands of seabirds are killed each year (Baker et al. 2007). On land, there are risks including mortality and habitat degradation associated with alien species (Seto and Conant 1996, Imber et al. 2000, Baker et al. 2002, Imber et al. 2003, Jouventin et al. 2003, Igual et al. 2006, Jones et al. 2008). Seabird demographic parameters, such as breeding success and survival, are also linked to environmental conditions (Baduini et al. 2001, Thompson and Ollason 2001, Weimerskirch et al. 2003, Ainley et al. 2005, Grosbois and Thompson 2005, Jenouvrier et al. 2005, Votier et al. 2005, Crespin et al. 2006, Delord et al. 2008), and climate change must be considered a threat (Croxall 2004, Boyce et al. 2006, Sutherland et al. 2006, Barbraud et al. 2008). Baker et al. (2002) provide a good overview of additional threats that seabirds face, such as over-extraction of prey-species, and chemical and physical pollution.

1.4 Potential biological removal of birds

One approach to species management is to determine the number of deaths that the population can sustain beyond natural mortality. In Chapter 2, a simple decision rule is presented to calculate the number of excess deaths that may be sustained, termed the potential biological removal (*PBR*). The *PBR* method is based on a rule designed for marine mammals,

$$PBR = \frac{1}{2} R_{\max} N_{\min} f$$

where $R_{\max}$ is the maximum annual net recruitment rate, $N_{\min}$ is a minimum estimate of population size (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).

Seabirds and many other bird species have similar life histories as 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 also relevant for seabirds. While the use of the *PBR* approach for seabirds has been alluded to in the literature (Hunter and Caswell 2005, Niel and Lebreton 2005), estimating $R_{\max}$ using typical matrix model approaches (Caswell 2001) can be difficult. This is because it requires a population undergoing rapid expansion or, alternatively, broad assumptions for the potential ranges of various parameters. Niel and Lebreton (2005) noted that work they had done using allometric relationships (Blueweiss et al. 1978, Allaine et al. 1987, Gaillard et al. 1989) to estimate the maximum growth rate for birds ($\lambda_{\max} = R_{\max} + 1$) given only adult survival (*s*) and age at first breeding (α) allowed the *PBR* method to be applied to birds if a population estimate was also available.

The *PBR* method requires relatively little information in order to make management decisions. It was initially developed for cetaceans and pinnipeds and there have been no adaptations when applying it to birds. In Chapter 2, I provide guidelines for appropriate use of the method and case studies comparing results from this method to other approaches, and *PBR* calculations for 22 species or sub-species of seabirds breeding in New Zealand are provided in Appendix A, based on available data. However, the population estimates used are imprecise (Brooke 2004a), and potentially subject to high levels of bias.

1.5 Population estimates

Breeding seabirds appear at colonies and non-breeding birds often do not (Baker et al. 2002). Because of this, the ‘population size’ of seabirds is often given by the number of breeding pairs (e.g. Woehler and Croxall 1997, Baker et al. 2002, Elliott and Walker 2005, Delord et al. 2008). For the *PBR* method to be applied, an estimate of the actual population size – not an index of it – must be available. Population estimates for albatrosses and petrels are based on the number of breeding pairs times a rule-of-thumb multiplier (Gales 1998, Taylor 2000, Brooke 2004a, Brooke 2004b). For example, Brooke (2004b) suggests a multiplier of 5 for long-lived seabirds who are annual breeders, but with no information about the potential uncertainty in the rule-of-thumb multiplier.

Complications to this extrapolation include uncertainty in survival rates and other demographic parameters. In particular, the proportion of adults that breed in a given year is unknown, as some breeding pairs may skip a year, and some bird species (those in *Diomedea*) breed biennially. Further, the proportion of birds breeding may vary substantially according to species (Chastel et al. 2005) and year (Cam et al. 1998, Chastel et al. 2005, Jenouvrier et al. 2005).

In Chapter 3, a simple population model is considered to provide an improved rule-of-thumb multiplier. Sets of demographic parameters for the model are generated by constraints placed on the asymptotic growth rate λ. This allows both a rule-of-thumb multiplier and its uncertainty to be calculated given only s, α, and λ. Uncertainty in the number of breeding pairs is also easily incorporated into a population estimate and into the 20th percentile estimate ($N_{\min}$) used in the *PBR* calculation. Combining uncertainty in the estimated number of breeding pairs and in the rule-of-thumb multiplier allows a more realistic assessment of the uncertainty in the population size of Procellariiformes than has been provided before, and means that the *PBR* method no longer requires an estimate of the total population size, but only of the number of breeding pairs.

1.6 Generation time and maximum growth rate

In order to calculate the maximum growth rate for birds, Niel and Lebreton (2005) relied on a simplified calculation of generation time. Generation time is important to calculating maximum annual growth rates because the intrinsic maximum growth rate per generation is approximately constant (Fowler 1988, Niel and Lebreton 2005). In addition to its role in the calculation of $\lambda_{\max}$, generation time can be used in a variety of other contexts, such as determining the sensitivity of a population to changes in adult survival or fecundity (Lebreton and Clobert 1993, Gaillard et al. 2005, Lebreton 2005) or studying evolution rates (Sarich and Wilson 1973, Martin and Palumbi 1993, Gillooly et al. 2005).

In order to calculate the mean generation length, age-specific survival and fecundity rates, and the population growth rate are generally required (Leslie 1966, Gaillard et al. 2005, Niel and Lebreton 2005). For many species, parameter estimates for juveniles may be difficult to estimate as they are often not present in the study area (Schwarz and Arnason 2000). This is particularly true for albatrosses and petrels, where non-breeding birds are typically at sea (Baker et al. 2002). Gaillard et al. (2005) and Niel and Lebreton (2005) were able to calculate mean generation time knowing only age at first breeding (α), adult survival (s) and annual growth rate (λ) by assuming constant fecundity and survival from the age at first breeding. However, in many populations – including Procellariiformes where not all animals begin breeding at the same age – fecundity increases over a number of years (Schwarz and Arnason 2000). In particular, data for 6 of the 13 bird species used by Niel and Lebreton (2005) suggested increasing fecundity with age.

In Chapter 4, I develop a simple calculation of generation time for any animal population that allows for increasing fecundity over time, but still does not require knowledge of juvenile survival. In this context, fecundity refers to overall reproductive output per animal, and increases with age may be due to an increase in the proportion of animals breeding, to improved breeding success, or to an increase in the number of offspring per female. The new calculation of generation time allows a modification of the calculation of $\lambda_{\max}$ for birds, when using the more general population model. Further, in the absence of detailed knowledge of age-specific fecundity, an ad hoc adjustment to age at first breeding can be used in the Niel and Lebreton (2005) allometric-based formula to achieve estimates of $\lambda_{\max}$ similar to those achieved by more standard matrix model approaches (Caswell 2001).

1.7 Estimating the mean age at first breeding

For Procellariiformes, where breeding birds produce one egg per year, variation in age-specific fecundity rates is primarily due to the delayed entry into breeding, and the mean age at first breeding is an obvious value to use as an ad hoc adjustment in the calculation of $\lambda_{\max}$. In Chapter 5, emphasis is placed on calculating the mean age at first breeding using capture-recapture data, with results applicable beyond the *PBR* method. Problems with using the observed mean age at first breeding related to study duration and emigration are discussed, using albatrosses as an example. The observed mean age at first breeding for albatrosses can have substantial negative bias (even with perfect detectability), and model-based estimates based should be used.

If certain assumptions about emigration are met, it is shown in Chapter 5 that Bayesian capture-recapture methods are capable of providing minimally biased estimates of age at first breeding and other parameters, even when parameters such as juvenile survival are unknown. However, the effect of the model used for recruitment may be large, and in studies of limited duration it may not be possible to distinguish between competing models. Because of this, model-based error can not be ignored. In addition to simple examples, capture-recapture data for Gibson's albatrosses (*Diomedea gibsoni*) is used to estimate the age at first return and breeding.

1.8 Summary

A rule-of-thumb tool was developed for calculating the number of additional mortalities that Procellariiformes can sustain given only adult survival, age at first breeding, the number of breeding pairs, and a management goal. This expands the work of Niel and Lebreton (2005) and Wade (1998) by recognizing limitations in the data available for albatrosses and petrels, and by combining knowledge of their population structure with population modelling tools to overcome those limitations. The suggested use for this is as a screening tool. For example, if estimated mortalities from all human-related sources are below the calculated threshold then they are likely sustainable; if they are greater than an upper limit then they are likely unsustainable. Levels of mortality in between these two values suggest that a more detailed study is necessary. Initial screening tools allow valuable research time and money to be directed towards species with the greatest need for additional research. In the final chapter, in addition to an overall discussion, tools developed in each chapter will be combined to calculate the *PBR* for Gibson's albatrosses given census data and using fecundity and survival estimates from capture-recapture data.

The benefits of this research extend beyond calculating the number of Procellariiformes that may be killed in fisheries. Threats to bird species come from a variety of sources, such as wind turbines (Everaert and Steinen 2007), power lines (Bevanger 1998), or motor vehicles (Forman and Alexander 1998), and the *PBR* approach can be applied to them as well. Knowledge of the population size of seabirds has more general applications, such as calculating their consumption of food (as in Brooke 2004b) or converting harvest levels to harvest rates, as well as being a basic population parameter. The formulas for generation time allow more accurate calculations than those provided by Gaillard et al. (2005) and Niel and Lebreton (2005) for species where fecundity differs by age class while still only using data likely to be available; these can be applied to any species. Finally, in addition to its use in calculating maximum growth rate, age at first breeding is a basic biological parameter important in the calculation of age-specific fecundities where appropriate care is necessary to achieve reliable estimates.

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Chapter 2. Estimating the ability of birds to sustain additional human-caused mortalities using a simple decision rule and allometric relationships

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 (2005) applied a simple decision rule (Wade 1998) 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* method 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.

2.1 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 work on fisheries bycatch of seabird species (primarily albatrosses and petrels, the Procellariiformes) in New Zealand where limited demographic information is available. Typically, demographic information is limited to rough estimates of the population size, adult survival, and 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 net 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 mean that minimal effort can provide valuable information 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 chapter are to describe the *PBR* method in detail and to explore the impact of uncertainty in the estimates used to calculate the *PBR*. Three examples of its use are provided. The first two involve the greater snow goose (*Anser caerulescens atlanticus*) and the magpie goose (*Anseranas semipalmata*), and allow results to be compared 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.

2.2 Methods

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

$$PBR = \frac{1}{2} R_{\max} N_{\min} f \tag{2.1}$$

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

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

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 for population growth (i.e. as N goes to 0 in this population model). In order to use Equation 2.1 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, Allaine 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.

2.2.1 Estimating $R_{\max}$

The maximum annual net recruitment rate ($R_{\max}$) and maximum annual population growth rate ($\lambda_{\max}$) are related by the equation $R_{\max} = \lambda_{\max} - 1$, and estimation is done via $\lambda_{\max}$. With appropriate demographic information, matrix population models can be constructed to estimate $\lambda_{\max}$ (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 ($\lambda_{\max}$) and the mean optimal generation length ($\overline{T}_{op}$) 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):

$$\ln\left(\lambda_{\max}\right)\overline{T}_{op} \approx 1$$

and

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

Combining these yields

$$\lambda_{\max} = \exp\left[\left(\alpha + \frac{s}{\lambda_{\max} - s}\right)^{-1}\right] \tag{2.2}$$

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 eleven bird species undergoing growth that the estimates from Equation 2.2 are similar to estimates achieved from matrix approaches ($r = 0.884$). 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 Figure 2.1.

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 $\lambda_{\max}$. Further, under the Niel and Lebreton method, exponential growth will occur as long as conditions are optimal (as is the case with the matrix approaches used to calibrate the method). Relating these growth rates to the theoretical maximum growth rate under density dependence (i.e. when N is close to 0) is one of many approximations used when combining the two approaches.

2.2.2 Calculating $N_{\min}$

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 ($\hat{\sigma}_{\hat{N}}$), an estimate and a coefficient of variation ($\widehat{CV}_{\hat{N}} = \hat{\sigma}_{\hat{N}} / \hat{N}$), 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 ($CV_{\hat{N}} = \sigma_{\hat{N}} / N$), where the p^{th} percentile estimate is given by

$$N_p = \hat{N} \exp\left(Z_p \sqrt{\ln\left(1 + CV_{\hat{N}}^2\right)} \right) \tag{2.3}$$

where Z_p is the p^{th} standard normal variate. Equation 2.3 is correct when $\hat{N}$ represents the median; if it represents the mean, the right-hand side must be divided by $\sqrt{1 + CV_{\hat{N}}^2}$. 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 ($\widehat{CV}_{\hat{N}}$) rather than a known one. The ratio of the two percentile estimates is

$$\frac{\hat{N}_p}{N_p} = \exp\left(Z_p \left(\sqrt{\ln\left(1 + \widehat{CV}_{\hat{N}}{}^2\right)} - \sqrt{\ln\left(1 + CV_{\hat{N}}{}^2\right)} \right) \right)$$

This difference may be small if $\widehat{CV}_{\hat{N}}$ is reasonably close to $CV_{\hat{N}}$, but can be substantial otherwise. For example, if $CV_{\hat{N}} = 0.5$ and $\widehat{CV}_{\hat{N}} = 0.4$, there is an 8% bias in $\hat{N}_{0.2}$, which increases to 21% for $\widehat{CV}_{\hat{N}} = 0.25$. Hereafter, it will be assumed that $CV_{\hat{N}} \approx \widehat{CV}_{\hat{N}}$, and the notation $CV_{\hat{N}}$ will be used throughout.

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,

$$\hat{N} = \sqrt{N_L N_U} \tag{2.4}$$

and,

$$CV_{\hat{N}} = \sqrt{\exp\left(\left(\frac{\ln\left(N_U / N_L\right)}{2Z_{1-\alpha/2}}\right)^2\right) - 1} \tag{2.5}$$

Equations 2.4 and 2.5 may then be used in Equation 2.3 to estimate N_p.

A Taylor series approximation, $\ln\left(1+CV_{\hat{N}}^2\right) \approx CV_{\hat{N}}^2$, may be used in Equation 2.3 to estimate $N_{\min} = \hat{N}_{0.2}$ as

$$N_{\min} = \hat{N}\exp\left(Z_{0.2} CV_{\hat{N}}\right) \tag{2.6}$$

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 Equation 2.6 with Equation 2.1 yields

$$PBR = \frac{1}{2} R_{\max} f \hat{N} \exp\left(Z_{0.2} CV_{\hat{N}}\right) \tag{2.7}$$

2.2.3 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.

2.2.4 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 Equation 2.1,

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

Using the estimate of $N_{\min}$ from Equation 2.6, this is re-written as

$$h_a = \frac{1}{2} R_{\max} f \exp\left(Z_{0.2} CV_{\hat{N}}\right) \tag{2.8}$$

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

$$h_{\max} = \frac{1}{2} R_{\max} \tag{2.9}$$

Thus, combining Equations 2.8 and 2.9, the ratio between the allowable harvest rate and maximum harvest rate, is

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

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.

2.2.5 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 Equation 2.7). 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 (*Thallasarche 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 (*Phalocracorax 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 Equation 2.2. 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. The Niel and Lebreton method recognizes the biological relationship between survival and fecundity, and in this method survival is numerically 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 (Figure 2.1), a counterintuitive relationship for those used to matrix models, where population parameters are controlled individually. Note that this inverse relationship means that the curves presented in Figure 2.1 include some combinations of s and α unlikely to be observed (e.g. low survival, and high age at first breeding does not occur). Further, caution is warranted for species where estimates of survival approach 1: $\lambda_{\max}$ quickly decreases in this region, so a small change in the estimate of s could lead to a large change in the estimate of $\lambda_{\max}$ and the *PBR.*

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 $\lambda_{\max}$ and *PBR*.

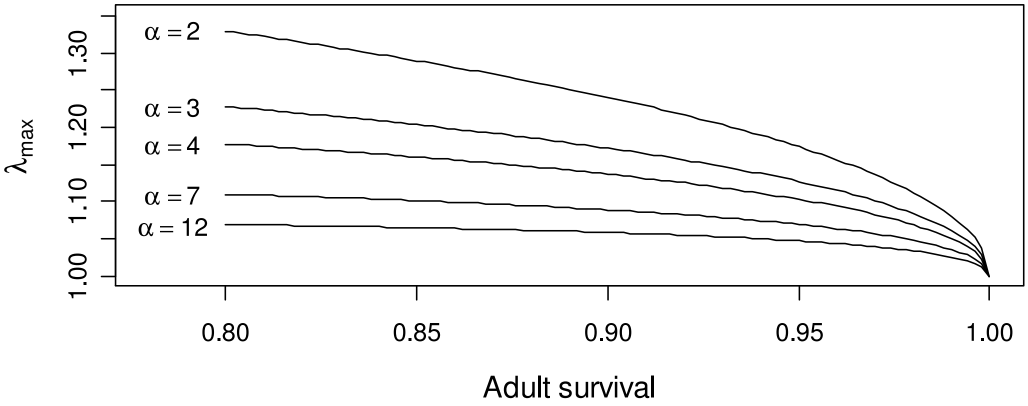

Figure 2.1. Maximum annual growth rate ($\lambda_{\max}$) as a function of age at first breeding (α) and adult survival estimated by the methods of Neil and Lebreton (2005).

2.3 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 $\lambda_{\max}$ 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. The *PBR* approach was also applied to other Procellariiformes of interest to New Zealand managers; a summary is provided in Appendix A.

2.3.1 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 1970-74, 1975-83, 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 $\lambda_{\max} \approx 1.21$ (Equation 2.2), 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 1990-98, 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 $\lambda_{\max} \approx 1.164$ (Equation 2.2); 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 $\lambda_{\max}$. 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),

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

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

$\hat{\lambda}_{\max} = \sum_{p=1}^{3} w_p \hat{\lambda}_{\max,p}$ and $\hat{\sigma}^2_{\lambda_{\max}} = \sum_{p=1}^{3} w_p^2 \hat{\sigma}^2_{\lambda_{\max,p}}$ 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, Equation 2.9 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 $\lambda \approx \lambda_{\max}\left(1-h\right) \Rightarrow \hat{h}_c = 1 - 1/\hat{\lambda}_{\max}$ by setting $\lambda = 1$ with approximate standard error $\hat{\sigma}_{h_c} \approx \hat{\sigma}_{\lambda_{\max}} \big/ \hat{\lambda}^2_{\max}$.

In addition to the growth and harvest rates used above, Menu et al. (2002) provided independent estimates of adult survival for the periods 1970-74 and 1984-98. 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 $\lambda_{\max}$ from Equation 2.2, 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,

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

Natural mortality was then estimated in an analogous manner to $\lambda_{\max}$, with weights based on the period length. Finally, while some birds begin breeding by age two, breeding propensity increased from 0.35 at age 3 to 0.77 and 0.85 at ages 3 and 4, respectively (Gauthier and Brault 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 Equations 2.2 and 2.8 to provide plausible ranges for $\lambda_{\max}$ 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 $p_\alpha = \{0.25, 0.50, 0.25\}$ and $s_0 \sim N\left(\hat{s}_0, \hat{\sigma}_{\hat{s}_0}\right)$. Finally, estimates of $\lambda_{\max}$ and the harvest rate necessary to control the population from the three approaches were compared.

2.3.2 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 annually), 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, the only estimates needed are age at first breeding, adult survival, conservation status, and population size to estimate $\lambda_{\max}$, 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 $N_{\min}$ (Equations 2.4, 2.5, and 2.6). 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 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 $\lambda_{\max}$, h_a, $h_{\max}$, and *PBR* to be calculated.

2.3.3 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 2009). 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-CAMLR 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 $CV_{\hat{N}} = 0.5$ 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 (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. I 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.

2.4 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 (Figure 2.1). For large waterfowl such as geese, $\lambda_{\max}$ may be near 1.2 (see examples in Niel and Lebreton 2005), while for seabird species such as Procellariiformes, $\lambda_{\max}$ is commonly less than 1.1, indicating that, even under optimal conditions, these populations can not grow faster than 7% (albatrosses), or 10% (petrels, shearwaters), in one 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 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%.

2.4.1 Greater snow geese

Maximum growth rates (estimate ± SE) using Eqs. (2.2 & 2.8) for greater snow geese were estimated from the census and harvest data for the 1970-74 (1.190 ± 0.032), 1975-83 (1.136 ± 0.016), and 1984-98 (1.165 ± 0.011) periods, which combined to

Table 2.1. Maximum growth rate ($\lambda_{\max}$) 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	$\lambda_{\max}$	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%)

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 Equation 2.9 (Table 2.1). Empirical estimates (± 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 1975-83 period, when high harvest rates resulted in low growth. Similarly, natural survival estimates (± SE) for 1970-74 (0.869 ± 0.045) and 1984-98 (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 $\lambda_{\max}$ and the *PBR* estimate of $h_{\max}$ (Eqs. 2.2 & 2.8) 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 2.1.

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 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 $\lambda_{\max}$ and h_c are largest when uncertainty is incorporated into Equations 2.2 and 2.8. This is quite reasonable, as these estimates are based on minimal information compared to the more sophisticated approaches available.

2.4.2 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 $\lambda_{\max}$ 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 (Equations 2.4, 2.5, and 2.6). 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 Equation 2.8 of $h_a=3.3\%$ (Equation 2.7), ranging from $h_a=2.6\%$ to $h_a=5.7\%$. Thus, while initial harvest rate estimates are similar to Brook and Whitehead (2005a, 2005b), 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.

2.4.3 White-chinned petrels

The approximately 7 million white-chinned petrels (Brooke 2004), and the assumption that $CV_{\hat{N}} = 0.5$, 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, 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 6,800 ($f = 0.1$) 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, and concerns about bycatch levels are justified.

2.5 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 Steinen 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 Equation 2.1, 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), $\lambda_{\max}$ 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 Procellariiformes – 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 Procellariiformes, 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 $\lambda_{\max}$ 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 $\lambda_{\max}$. However, the *PBR* method, combined with the Niel and Lebreton method for estimating $\lambda_{\max}$, requires very little information in order to arrive at a decision and is easy to calculate. 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 $\lambda_{\max}$ is available, whether it is from Equation 2.2, a matrix approach, or from census data. However, direct estimation of $\lambda_{\max}$ 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 $\lambda_{\max}$, due to the number of parameters that need to be estimated. The Niel and Lebreton method is limited by the assumption that all breeding age classes have a constant fecundity rate. However, in Chapter 4 an adjustment to the estimate of $\lambda_{\max}$ is developed when fecundity changes with age; it is also shown that ad hoc adjustments to α, as used by Niel and Lebreton (2005), work reasonably well.

The Niel and Lebreton (2005) estimate of $\lambda_{\max}$ 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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Chapter 3. Population estimation of albatrosses and petrels with minimal demographic information

Seabirds such as albatrosses and petrels (the Procellariiformes) are frequently caught in longline and trawl fisheries, and accurate assessments of the population size will help determine the level to which they are impacted. An approach to assessing the potential for seabirds to sustain additional mortalities given only adult survival (s), age at first breeding (α), a minimum population estimate, and conservation goal is available (the *PBR* approach: see Chapter 2, Wade 1998, and Niel and Lebreton 2005). While s and α may be available or reasonably inferred for seabirds, population estimates are typically based on limited data and educated guesses, extrapolated from the number of breeding pairs. This chapter provides an approach to population estimation for Procellariiformes given s, α, and the number of breeding pairs (B).

The approach is based on building a simple population model and considering the sets of parameter values that lead to plausible asymptotic estimates of the growth rate λ. A Markov Chain Monte Carlo (MCMC) approach is developed for fast simulation. The estimates of λ, together with an estimate of the number of breeding pairs, lead to a set of plausible population estimates conditional on the original population model. Additional robustness may be developed by considering multiple population models. These can be used to estimate a minimum population size and, importantly, bounds on the population size. Estimates are based on asymptotic results assuming constant values for s, α and breeding parameters, and will perform better for populations with limited temporal variation. Combined with the *PBR* approach, this allows at least a rough assessment of the potential for Procellariiformes to sustain additional mortalities given only s and α, and the number of breeding pairs.

3.1 Existing population estimation methods

Procellariiformes begin life as well-tended chicks, spend several years away as juveniles, return either to their natal colony or elsewhere as pre-breeders, and, if successful at acquiring a mate, become breeders. Breeding pairs attempt to raise, at most, one chick annually (with the exception of a few small tropical species not considered here; Brooke 2004). However, not all adult birds are breeders, and breeders may skip breeding for a year, so there is also a group of non-breeding adults. For many populations, little is known about the numbers of juveniles, pre-breeders, and non-breeding adults.

Estimates of the number of breeding pairs usually refer to *per annum* breeding pairs and omit skipping breeders, rather than the total number of pairs that sometimes breed. In particular, breeding pairs belonging to *Diomedea* skip breeding the year after breeding successfully yet are still part of a breeding pair. Non-breeding adults are then potentially composed of two groups of birds; the first group are those that bred successfully in the previous year and are therefore obligate non-breeders, and the second group are other non-breeders, which includes both mature birds who are not currently members of a breeding pair as well as members of a breeding pair who skip breeding even though they are not obligate non-breeders.

For many seabirds, current population estimates are imprecise (Baker et al. 2002, Brooke 2004a) and are based on the number of breeding pairs times a rule-of-thumb multiplier (Gales 1998, Taylor 2000, Brooke 2004a, Brooke 2004b). Many available estimates in compilations about seabirds (Taylor 2000, Brooke 2004a, BirdLife International 2009) come from Gales (1998), which does not specify the methodology used in calculating the multiplier. Brooke (2004b) suggests a multiplier of 5 for long-lived seabirds who are annual breeders, based on a simple population model with assumed parameter values. There appears to be no information about the potential variability in any of the rule-of-thumb multipliers.

In the primary literature, population size of seabirds is often used interchangeably or near-interchangeably with the number of breeding pairs (e.g. Woehler and Croxall 1997, Baker et al. 2002, Elliott and Walker 2005, Delord et al. 2008). This is because many standard methods of estimating animal abundance (Schwarz and Seber 1999) are not applicable, as typically only breeding birds appear at colonies (Baker et al. 2002). Information limited to the number of breeding pairs may be helpful in looking at population trends (as in Woehler and Croxall 1997, Elliott and Walker 2005, Delord et al. 2008). However, there may be substantial variability in the proportion of birds breeding in a given year (Cam et al. 1998, Chastel et al. 2005, Jenouvrier et al. 2005). Thus, short-term trends in the number of breeding pairs may not be related to trends in the population size, while the long-term relationship between the number of breeding pairs and population size may not be linear.

Chastel et al. (1995) studied three seabird species and found that body condition could influence both breeding success and the proportion of experienced breeders not breeding. In addition to entirely skipping breeding, some birds also abandoned eggs early in the nesting season. The longest-lived species in the study, the blue petrel

(*Halobaena caerulea*), had the highest variability in the number of non-breeding adults, suggesting that they prefer to reduce reproductive effort to increase survival probability (Chastel et al. 1995). This suggests that counts of the short-term number of breeding pairs, especially for long-lived birds such as albatrosses and large petrels, could be influenced by environmental conditions rather than a change in population size. For example, Elliott and Walker (2005) observed a *c.* 50% increase in the number of nests of the Antipodean albatross (*Diomedea antipodensis*) on Antipodes I. between 2001 and 2004. However, the maximum annual growth rate for this species is around 4% (Appendix A), suggesting that the observed increase was not due to intrinsic population growth alone.

Further, the proportion of non-breeding experienced breeders varies considerably between species (Chastel et al. 1995). It is possible that the average proportion of non-breeding adults is related to population density (i.e. density-dependent). In order to assess the ability of a population to sustain additional mortalities, an actual population estimate is needed. This suggests that any rule-of-thumb multiplier relating the number of observed breeding pairs to the total population size needs to account for uncertainty in the proportion of non-breeding adults.

3.2 Matrix population models

A common tool used in population modelling is matrix population models (Leslie 1945, Leslie 1948, Lefkovitch 1965, Caswell 2001, Lebreton 2005). These are especially useful for Procellariiformes, as the discrete time nature of matrix models is consistent with the annual (or biennial) breeding cycle. Matrix population models may be categorised as age-based (Leslie 1945, 1948), stage-based (Lefkovitch 1965), or both (Lebreton 2005). Age-based models are used to track the population using age classes (e.g. the number of one-year olds, two-year olds, or three-year olds or older). Stage-based models are used when the population is better characterised by developmental stages (i.e. seeds, immature plants, mature plants). Procellariiformes experience distinct stages, but these are closely linked to age, and so could be modelled using either approach. Alternatively, age-by-stage-based models, which consider both the age and the stage of population members, could be employed. In these models, for example, a seven-year old bird that had returned to the colony but not yet begun to breed would be modelled differently than a seven-year old bird that had begun to breed. Lebreton (2006) and Caswell (2001) provide good reviews of matrix models.

All of these discrete time models follow the form

$$\vec{a}_{t+1} = P\left(\vec{\theta}\right)\vec{a}_t$$

where $P\left(\vec{\theta}\right)$ is a square projection matrix whose entries relate to transition probabilities from one age/stage category to another (i.e. in an age-based matrix, the *i,j*th entry is the probability of surviving from age *i* to age *j*; when $j = 1$, the entries relate to fecundity) which may depend on parameters $\vec{\theta}$; and $\vec{a}_t$ is the number of animals in each age-, stage-, or age-by-stage- category in year *t*. The total population size at time *t* is $N_t = \left|\vec{a}_t\right|$.

3.2.1 Transition matrix structure

Common choices for $\vec{\theta}$ (Lebreton 2006) include time (i.e. $P\left(\vec{\theta}\right) = P_t$ is a random environment matrix) or N_t (i.e. $P\left(\vec{\theta}\right) = P\left(N_t\right)$ is a density-dependent model). The simplest model is one where $P\left(\vec{\theta}\right)=P$ is a constant matrix. In some cases, a more complex model can be reasonably represented by a simpler one. For example, a density-dependent model $P\left(\vec{\theta}\right)=P\left(N_t\right)$ may be closely approximated by $\hat{P}=P\left(N\right)|_{N=N_t}$ for N in the region of N_t. In other words, as long as the population does not change much, a simple fixed projection matrix may be used in place of a more complex density-dependent one. While the complex model may be more biologically plausible, a simpler model can be easier to interpret and its parameters may be computationally easier to estimate with available data. However, like any extrapolation, if the matrix model is used to make projections far from the region of estimation, use of the simpler model may yield unrealistic results.

For Procellariiformes, any biologically plausible model, that tries to capture intricate nuances, would be complex. It should include different stages, such as chicks, at-sea juveniles, prospecting pre-breeders, and adults. Adults would also be characterised by their state (i.e. breeders, obligate non-breeders, otherwise skipping breeders, or long-term non-breeders). The difference between stage and state is somewhat subtle (and mathematically ignorable). Birds progress from one stage to another, but never go backwards. That is, a pre-breeder may remain a pre-breeder or become an adult, but can not return to being a juvenile. States, on the other hand, do not have this limitation. A breeding adult one year may become an obligate non-breeder the next, an otherwise skipping breeder the following year, and a breeder again the year after.

Transition rates between stages for Procellariiformes should be age-dependent. For example, a 2-year old juvenile albatross is not ready to become a prospecting pre-breeder, while a 7-year old one likely is. Further, these transition rates may be density-dependent. For example, it is reasonable to assume that in low-density conditions, a younger bird may be able to find a high-quality nesting location, whereas in high-density conditions it may be more difficult. Transition rates between adult states may not be (or may be minimally) age-dependent. However, they are likely to vary according to environmental conditions (Chastel et al. 1995, Cam et al. 1998, Jenouvrier et al. 2005). In general, parameters that the population is sensitive to, such as adult survival, are likely to not vary greatly, while parameters that the population is insensitive to, such as breeding success, are likely to be more stochastic (Gaillard et al. 1998, Doherty et al. 2004).

The lack of data available for many species of Procellariiformes requires the use of a much simpler model, even though it is reasonable to assume that there is density-dependence and environmental stochasticity. Further, while Procellariiformes go through distinct stages, these stages are predominantly described by age differences. Transition rates between adult states may ultimately be reduced to the proportion of adult birds that breed in a given year. A simplification used here is to assume that that proportion is constant. Hence, a simple age-based population model with a constant projection matrix will be used.

3.3 Simple population models for seabirds

In Niel and Lebreton (2005), a population model was selected that assumes constant fecundity and constant adult survival (s) after age of first reproduction (α). Consistent with their model, an age-based population model was assumed, where all birds become adults at age α, adult survival and juvenile/pre-breeder survival (s_J)

are constant, and a constant proportion (k) of birds of each age class breed each year with success b. Breeding success includes all sources of mortality to age 1. Fecundity is then equal to $kb/2$. This model is summarized by the projection matrix

$$P = \begin{bmatrix} 0 & \cdots & 0 & kb/2 \\ s_J & 0 & \cdots & 0 \\ 0 & \ddots & 0 & 0 \\ 0 & 0 & s_J & s \end{bmatrix} \tag{3.1}$$

In addition, two further constraints are imposed. Since b represents all sources of mortality to age 1, and it is reasonable to assume that this period is the highest mortality period the birds will encounter, it is assumed that $b < s_J$. Further, it is assumed that juveniles/pre-breeders have a higher mortality rate than adults, so $s_J < s$. An alternative model for juvenile survival will be considered later. Also note that seabirds recruit to the breeding population over a number of years, and the assumption of constant fecundity from age α is an obvious simplification. Use of an approximate value, such as mean age at first breeding, is suggested.

A common use of the projection matrix is to estimate the finite rate of increase λ of the population from the dominant eigenvalue of P, and the population structure from the associated eigenvector (Caswell 2001, Skalski et al. 2007). Thus, if $a_t^{(i)}$ is the number of birds of age *i* in the *t*th year, and $\vec{a}_t = \begin{bmatrix} a_t^{(1)} & \cdots & a_t^{(\alpha-1)} & a_t^{(\alpha+)} \end{bmatrix}^T$ and $a_t^{(\alpha+)}$ is all birds of age α or greater, then $\vec{a}_{t+1} = P\vec{a}_t$, and λ may be calculated in a straightforward manner. The associated right eigenvector is proportional to the stable population structure $\vec{p} = \begin{bmatrix} p^{(1)} & \cdots & p^{(\alpha-1)} & p^{(\alpha+)} \end{bmatrix}^T$, where $p^{(i)}$ is the proportion of birds in the *i*th age class. Combining this with the number of breeding pairs (B) and the proportion of birds breeding allows estimates of the adult population size ($a^{(\alpha+)}$) and total population size (N) where

$$a^{(\alpha+)} = \frac{2B}{k}$$

and

$$N = \frac{a^{(\alpha+)}}{p^{(\alpha+)}}$$

That is, given $B, \alpha, s, s_J, k, b, \lambda$, then N is determined uniquely, or

$$N = g\left(B, \alpha, s, s_J, k, b, \lambda\right)$$

For example, a population with juvenile survival $s_j = 0.9$, adult survival $s = 0.95$, age of first breeding $\alpha = 5$, breeding success $b = 0.8$, and proportion breeding $k = 0.5$ is summarized by

$$P = \begin{bmatrix} 0 & 0 & 0 & 0 & 0.2 \\ 0.9 & 0 & 0 & 0 & 0 \\ 0 & 0.9 & 0 & 0 & 0 \\ 0 & 0 & 0.9 & 0 & 0 \\ 0 & 0 & 0 & 0.9 & 0.95 \end{bmatrix}$$

From this, the asymptotic growth rate and proportion adults are $\lambda = 1.056$ and $p^{(\alpha+)} = 0.62$. If the number of breeding pairs was $B = 1000$, then

$a^{(\alpha+)} = \dfrac{2 \cdot 1000}{0.5} = 4000$ and $N = \dfrac{4000}{0.62} = 6,452$.

3.3.1 Population estimation using geometric series

Because of the simple population model used, computational efficiency may be gained by noting that the population structure may be estimated using a simple geometric series, rather than using a built-in function that calculates eigenvectors. Let

$a^{(i)}$ be the number of birds in the *i*th age class (in an arbitrary year), so $N = \sum_{i=1}^{\infty} a^{(i)}$ (only birds at least one year old are counted). With the assumption of a constant proportion of non-breeders among different age classes, $B = \frac{1}{2} k \sum_{i=\alpha}^{\infty} a^{(i)}$, and the number of non-breeders (Q) is $Q = (1-k)\sum_{i=\alpha}^{\infty} a^{(i)}$. Also, the number of juveniles and pre-breeders (J) is $J = \sum_{i=1}^{\alpha-1} a^{(i)}$.

For a stable population with growth rate λ, the number of birds in the *i*th age class in year t_1 ($a^{(i,t_1)}$) is related to the number of birds in the *i*th age class in year t_2 ($a^{(i,t_2)}$) by

$$a^{(i,t_1)} = a^{(i,t_2)} \lambda^{t_1 - t_2}$$

Also, for $i \geq \alpha$, and assuming constant adult survival, $a^{(i,t)} = a^{(\alpha, t-(i-\alpha))} \cdot s^{i-\alpha}$. Thus, for a given year,

$$a^{(i)} = a^{(\alpha)} \cdot \left(\frac{s}{\lambda} \right)^{i-\alpha}$$

Assuming $\lambda > s$, a geometric series results for the number of breeding pairs,

$$B = \frac{1}{2} k \sum_{i=\alpha}^{\infty} a^{(\alpha)} \cdot (s/\lambda)^{i-\alpha} = \frac{1}{2} k a^{(\alpha)} \sum_{k=0}^{\infty} (s/\lambda)^{k}$$

or

$$B = \frac{k a^{(\alpha)}}{2(1 - s/\lambda)}$$

Rearranging,

$$a^{(\alpha)} = 2B(1 - s/\lambda)/k$$

Also, note that

$$Q = 2B(1-k)/k$$

Finally, for $i < \alpha$, $a^{(i)} = a^{(\alpha)} \big/ \left(s_J/\lambda\right)^{\alpha-i}$. Thus,

$$J = \sum_{i=1}^{\alpha-1} a^{(i)} = \sum_{i=1}^{\alpha-1} a^{(\alpha)} \big/ \left(s_J/\lambda\right)^{\alpha-i},$$

or, simplifying,

$$J = a^{(\alpha)} \sum_{i=1}^{\alpha-1} \left(\lambda/s_J\right)^i$$

Combining yields

$$J = \frac{2B\left(1-s/\lambda\right)\sum_{i=1}^{\alpha-1}\left(\lambda/s_J\right)^i}{k}$$

The number of adults is estimated as

$$N_A = 2B + \frac{2B\left(1-k\right)}{k} = \frac{2B}{k}$$

and the total population as

$$N = \frac{2B}{k} + \frac{2B\left(1-s/\lambda\right)\sum_{i=1}^{\alpha-1}\left(\lambda/s_J\right)^i}{k},$$

or

$$N = \frac{2B}{k}\left(1 + \left(1-s/\lambda\right)\sum_{i=1}^{\alpha-1}\left(\lambda/s_J\right)^i\right) \tag{3.2}$$

3.3.2 Incorporating uncertainty in *B*

In most practical circumstances, B is unknown, but an estimate ($\hat{B}$) and estimated coefficient of variation ($CV_{\hat{B}} = \sigma_{\hat{B}} \big/ E\left(\hat{B}\right) \approx \hat{\sigma}_{\hat{B}} \big/ \hat{B}$) may be available. Wade (1998, Equation 3) assumed that population estimates have a log-normal sampling distribution. In an analogous manner, if B follows a log-normal distribution with expected value $\hat{B}$ and setting $CV_B = CV_{\hat{B}}$, the underlying number of breeding pairs may be simulated as

$$B = \exp\left[\ln\left(\frac{\hat{B}}{\sqrt{1+CV_B^2}}\right) + x\sqrt{\ln\left(1+CV_B^2\right)}\right] \tag{3.3}$$

where $x \sim N(0,1)$ and $CV_B = \hat{\sigma}_{\hat{B}} / \hat{B}$. This allows uncertainty in B to be incorporated into population estimates.

3.3.3 Alternative model

Assuming that survival characteristics are learned over time, the assumption of constant juvenile survival to age α followed by a single step is naive. A second model is considered where survival is constant for all birds age 1 or older, with projection matrix

$$P^* = \begin{bmatrix} 0 & 0 & \cdots & 0 & kb/2 \\ s & 0 & \ddots & \vdots & 0 \\ 0 & s & \ddots & 0 & \vdots \\ \vdots & \ddots & \ddots & 0 & 0 \\ 0 & \cdots & 0 & s & s \end{bmatrix} \tag{3.4}$$

For Procellariiformes, it is reasonable to assume that young birds are naturally more vulnerable than adults, but that birds develop adult survival skills prior to breeding age. Thus, P and P^* represent two bounds of plausibility for juvenile survival rates in this type of population model, with a best model somewhere in between. The effect of using one population model instead of the other will be assessed to determine if it has a large impact on the population multiplier.

3.4 Parameter estimates for the population models

For many species, capture-recapture data is collected to estimate survival rates and age at first breeding. This data comes from birds banded as adults (typically breeding birds) as well as from birds banded as chicks. Because birds banded as adults are typically members of a breeding pair and birds banded as chicks spend several years away from the colony before returning (not necessarily to the study area), this data can not provide direct estimates of the population size (such as via the Lincoln-Peterson estimator) of juveniles and non-breeding adults, especially long-term non-breeding adults. However, the estimates of survival and age at first breeding, together with several simplifying assumptions, do allow an estimate of the population size to be made via the development of a population model and through a Markov Chain Monte Carlo (MCMC) simulation approach.

If parameter estimates and a covariance matrix are available for all parameters, then it is relatively straightforward to calculate approximate confidence intervals for λ and N via the delta method (Skalski et al. 2007). Alternatively, if samples from a joint distribution are available, bootstrap methods can used to estimate λ and N (Meyer et al. 1986). In practice, estimates are often available for s, α, and B, may be available for b, and would be rarely available for s_J (Lebreton 2001). Further, k is generally unknown; if there is a large pool of long-term, non-breeding adults, it would be impossible to estimate using current capture-recapture approaches.

In this chapter, it is assumed that there are estimates for s, α, and B, but not for b, k, and s_J. N is the parameter of primary interest, but both λ and N need estimates of all the other parameters in order to be estimated. The distribution of λ may or may not be known. If it is, a distribution for N may be calculated. However, even if it is unknown, long-lived seabirds can not grow faster than 5-10% per year, and, in many cases, it may be reasonable to assume that λ is somewhat near 1. In this case, a distribution for N conditional on λ may be calculated.

3.4.1 Constraints on breeding success for biennial breeders

The existence of an obligate non-breeder state for some albatrosses places a constraint between breeding success and the proportion of adults breeding – as breeding success increases, a greater proportion of adults become obligate non-breeders. Adult birds may then be characterised by three states: breeders (1), obligate non-breeders (2), or other non-breeders (3). The constraint between *b* and *k* may then be calculated (approximately) by considering the state structure of the adult birds.

The number of birds of age *i* ($a^{(i)}$, $i \geq \alpha$) is divided into adult breeders ($a^{(i,1)}$), obligate non-breeders ($a^{(i,2)}$), and other non-breeders ($a^{(i,3)}$). Let k_i be the proportion of birds of each age class that is breeding,

$$k_i = \frac{a^{(i,1)}}{a^{(i,1)} + a^{(i,2)} + a^{(i,3)}}$$

In this population model, $k_i = k_j = k \ \forall i, j \geq \alpha$, so

$$k = \frac{a^{(i,1)}}{a^{(i,1)} + a^{(i,2)} + a^{(i,3)}} = \frac{a^{(j,1)}}{a^{(j,1)} + a^{(j,2)} + a^{(j,3)}} \tag{3.5}$$

Clearly, there can be no obligate non-breeders of age α, so the state structure can not be constant across age classes. However, simulations using a slightly modified projection matrix that included state to state transitions suggest that the proportion of birds in each state becomes approximately constant fairly quickly unless a large proportion of birds do not begin breeding until later age classes (see Section 5.7.2 for further details). Further, assuming that the proportion of birds in each state is constant across age classes has minimal impact on the estimated population size relative to other sources of error in this study.

Thus, a reasonable approximation is that the proportion of birds in each state is constant across age classes and time, or,

$$\frac{a_t^{(i,\psi)}}{a_t^{(i)}} \approx \frac{a_{t+1}^{(j,\psi)}}{a_{t+1}^{(j)}} \text{ for } \psi \in \{1,2,3\}, \forall i, j, t \tag{3.6}$$

Noting that the number of birds of the next age class in each state from one year to the next is diminished by death only, yields

$$a_{t+1}^{(i+1,\psi)} \approx s a_t^{(i,\psi)} \text{ for } \psi \in \{1,2,3\} \tag{3.7}$$

Further, the number of obligate non-breeders of age $i+1$ in year $t+1$ is determined by the successful breeders age i in year t who survive,

$$a_{t+1}^{(i+1,2)} = a_t^{(i,1)} bs \tag{3.8}$$

Next, let $\eta = a^{(.,n)} / a^{(.,b)}$ ($\eta \geq 0$) be the ratio of breeding adults to other non-breeders, constant across age classes and years. Combining Equations 3.5 to 3.8 yields

$$\begin{aligned} k &= \frac{a_t^{(i,1)}}{a_t^{(i,1)} + a_t^{(i,2)} + a_t^{(i,3)}} = \frac{a_{t+1}^{(i+1,1)}}{a_{t+1}^{(i+1,1)} + a_{t+1}^{(i+1,2)} + a_{t+1}^{(i+1,3)}} \\ &\approx \frac{a_t^{(i,1)} s}{a_t^{(i,1)} s + a_t^{(i,1)} bs + a_t^{(i,1)} \eta s} = \frac{1}{1+b+\eta} \end{aligned} \tag{3.9}$$

This provides the constraint that $k \in \left[0, 1/(1+b)\right]$.

3.5 MCMC simulation

Markov chain Monte Carlo (MCMC) methods are used to estimate the population size for two models, one for biennially breeding albatrosses and one for all other petrels (including annually breeding albatrosses such as mollymawks). There are a variety of approaches that could be used to calculate sets of possible parameter values needed to estimate N. MCMC simulation can be easily implemented using freeware; these analyses used the OpenBUGS variant (Thomas et al. 2006, version 3.0.3) of BUGS (Lunn et al. 2000), linked to R (R Development Core Team 2008, version 2.7.0) using the R2WinBUGS library (Sturtz et al. 2005).

Bayes' Theorem and laws of conditional probability may be used to estimate the distribution for $N = g\left(B, \alpha, s, s_J, k, b, \lambda\right)$. In order to do this, the joint distribution $f\left(B, \alpha, s, s_J, k, b, \lambda\right)$ must be estimated. To do this, note that

$$\begin{aligned} f\left(B, \alpha, s, s_J, k, b, \lambda\right) &= f\left(s_J, k, b \mid B, \alpha, s, \lambda\right) f\left(B, \alpha, s, \lambda\right) \\ &= f\left(s_J, k, b \mid \alpha, s, \lambda\right) f\left(B, \alpha, s, \lambda\right) \end{aligned}$$

Next, an MCMC approach is used to calculate

$$f\left(s_J, k, b \mid \alpha, s, \lambda\right) \propto f\left(\alpha, s, \lambda \mid s_J, k, b\right) f\left(s_J, k, b\right)$$

noting that

$$f\left(\alpha, s, \lambda \mid s_J, k, b\right) \propto \begin{cases} 1 \text{ if } 0 = \lambda^{\alpha-1}\left(s-\lambda\right) + s_J^{\alpha-1} kb/2 \\ 0 \text{ otherwise} \end{cases} \tag{3.10}$$

where $0 = \lambda^{\alpha-1}\left(s-\lambda\right) + s_J^{\alpha-1} kb/2$ comes from solving the characteristic equation, where expansion around the first row results in determinants of triangular matrices,

$$0 = \det\left(P-\lambda I\right) = \det\begin{bmatrix} -\lambda & 0 & \cdots & 0 & kb/2 \\ s_J & -\lambda & \ddots & \vdots & 0 \\ 0 & s_J & \ddots & 0 & \vdots \\ \vdots & \ddots & \ddots & -\lambda & 0 \\ 0 & \cdots & 0 & s_J & s-\lambda \end{bmatrix}$$

$$= \left(-\lambda\right)\det\begin{bmatrix} -\lambda & 0 & \cdots & \cdots & 0 \\ s_J & -\lambda & \ddots & \vdots & 0 \\ 0 & s_J & \ddots & 0 & \vdots \\ \vdots & \ddots & \ddots & -\lambda & 0 \\ 0 & \cdots & 0 & s_J & s-\lambda \end{bmatrix} + \left(-1\right)^{1+\alpha}\left(kb/2\right)\det\begin{bmatrix} s_J & -\lambda & 0 & \cdots & 0 \\ 0 & s_J & -\lambda & \ddots & \vdots \\ \vdots & \ddots & s_J & \ddots & 0 \\ \vdots & \ddots & \ddots & \ddots & -\lambda \\ 0 & \cdots & \cdots & 0 & s_J \end{bmatrix}$$

$$= \left(-\lambda\right)^{\alpha-1}\left(s-\lambda\right) + \left(-1\right)^{\alpha-1} s_J^{\alpha-1} kb/2, \text{ or}$$

$$0 = \lambda^{\alpha-1}\left(s-\lambda\right) + s_J^{\alpha-1} kb/2$$

Use of MCMC methods provides an efficient method of estimating $f\left(s_J, k, b \mid \alpha, s, \lambda\right)$ and $f\left(N \mid \alpha, s, \lambda, B\right)$. In some cases, it is useful to study the population distribution given α, s, B ($f\left(N \mid \alpha, s, B\right) = f\left(N \mid \alpha, s, \lambda, B\right) f\left(\lambda\right)$); in most cases, the distribution conditional on λ will be of more interest, especially when little is known about the distribution of λ.

3.5.1 Petrel model

For the petrel model, given $\alpha, s, \hat{B}, CV_B$ and a range of realistic values for λ ranging from $\left[\lambda_L, \lambda_U\right]$ the following priors were assigned:

$$b \sim U\left(0, s_J\right)$$

$$k \sim U\left(0,1\right)$$

$$s_J \sim U\left(0, s\right)$$

$$\lambda \sim U\left(\lambda_L, \lambda_U\right)$$

These priors are vague because little is known about possible boundary values. So while $s_J = 0$ is clearly not plausible, it is unclear what the lower value would be. Instead, restrictions on λ inherently create constraints for the other parameters.

Any large value may be used for λ_U, as constraints on survival and other parameters naturally create an upper bound that may be achieved. For Procellariiformes, this value is reasonably close to Niel and Lebreton's (2005) dimensionless estimate ($\lambda_{\max}$; Equation 2.2). When setting the lower bound (λ_L), biological plausibility should be considered. This can be considered through an argument about generation time or fecundity. For example, if $s = 0.93$ and $\alpha = 6$, as might be reasonable for a petrel, if $\lambda = 0.95$ then $s_J > 0.56$ (Equation 3.10). This value is quite low and probably unrealistic, but it also unrealistic that the population would be decreasing at such a rate with $s = 0.93$ – this requires either very poor juvenile survival as above or minimal fecundity. If $s_J = 0.88$ and $\lambda = 0.95$ then fecundity across all adults is $kb/2 = 0.06$, implying a very low proportion of adults breeding, very poor breeding success, or both. This is due to the high sensitivity of petrel populations to changes in adult survival, and low values of λ are easily explained by a decrease in adult survival. On the other hand, as s approaches λ, a decreasing proportion of adults need to breed to support the population (i.e. $k \to 0$), and the population estimate becomes unrealistic (i.e. $\lim_{s \to \lambda} N = \infty$). In other words, $\lambda = s + 0.02$ implies an unrealistic and fundamental shift in breeding behaviour (compared to a growing population) where nearly all adults do not breed, or where breeding success is habitually low.

The minimum values for s_J, b, and k increase with λ, becoming biologically plausible when λ is greater than s by some amount. For example, for a stable population ($\lambda = 1$) with $s = 0.93$, then $s_J > 0.72$, which is in the range of plausibility. Further, the minimum value only occurs when $k = 1$ and $b = s_J$, so in most simulations s_J would be well above the minimum value. Placing a bound on λ_L is, to some extent, arbitrary. Noting that generation time for this population model is $\overline{T} = \alpha + s/(\lambda - s)$ (Niel and Lebreton 2005), and placing a fairly weak constraint that the maximum plausible generation time is no greater than 40, suggests that $\lambda_L = s + 0.0275$ is reasonable.

Next, $\det(P - \lambda I)$ was calculated using Equation 3.10, and

$$0 \sim U\left(\det(P - \lambda I) - \delta, \det(P - \lambda I) + \delta\right)$$

for some small tolerance value δ (set to 0.01); this step forces matrix model parameters that yield the correct λ. The value of δ in the final step determines accuracy (smaller is better) and computational speed (too small and most trial parameter values are rejected). The population size was calculated using Equation 3.2.

Initial values were calculated by setting $\lambda = 1$, drawing $s_J \sim U(s - 0.05, s)$, $b \sim U(0.4, s_J)$, and using the characteristic equation to calculate

$$k = \frac{2\lambda^{\alpha-1}(s - \lambda)}{s_J^{\alpha-1} b}$$

This could lead to $k > 1$, so the algorithm was iterated until $k \in [0,1]$. WinBUGS code for implementing this model for petrels is given in Section 3.9.

The number of breeding pairs was generated by sampling $x \sim N(0,1)$ and using Equation 3.3. The analysis was run for a variety of values of s and α, and results are presented conditional on λ. For the purposes of presentation, posterior values of λ were placed into bins of length 0.005 and centred conveniently at $1 \pm 0.005k$ for integer values of k, with the first bin centred at $s + 0.03$.

The population size (N) per breeding pair was estimated (Equation 3.2), along with various quantiles of the estimate. This relates to the rule-of-thumb multiplier that should be used given the number of breeding pairs. A total population estimate ($\hat{N}$) that incorporates uncertainty in the number of breeding pairs (Equation 3.3) was also calculated for $CV_B = 0.25$ and $CV_B = 0.5$. Of particular interest were the mean estimates for $\hat{N}$ and the 20th percentile estimates ($N_{\min}$) for use in *PBR* calculations.

3.5.2 Albatross model

The model for biennial breeding albatrosses is based on the petrel model, with a minor modification. Using the constraints from Equation 3.9, a prior is placed on η where

$$\eta \sim U(0,10000)$$

and the proportion of birds breeding is determined as $k = 1/(1+b+\eta)$. Similar to the petrel model, initial values were calculated by setting $\lambda = 1$, drawing $s_J \sim U(s-0.05, s)$, $b \sim U(0.6, s_J)$, and using the characteristic equation (Equation

3.10) to calculate k and then η. This approach was iterated until $k \in \left[0, 1/(1+b)\right]$. WinBUGS code for implementing this model for albatrosses is given in Section 3.9.

3.6 Modelled population estimates for Procellariiformes

The population model allowed assessment of both N and $N_{\min}$ given s and α, as well as other percentiles, N_p. Additional parameters, such as the number of adults or juveniles, were also easily monitored. Population estimates varied with λ (Figure 3.1), and became unstable as λ approached s, with unrealistically low levels of juvenile survival, proportion of adults breeding, and breeding success all possible. However, populations of Procellariiformes are so sensitive to adult survival that $\lambda \to s$ is unrealistic.

Population estimates decrease as λ increases (Figure 3.1), as the growth rate places constraints on the proportion of adults breeding (Figure 3.2) and other parameters. That is, a population can not grow quickly with low juvenile survival, breeding success, and proportion of adults breeding. However, the percentile bounds converge towards the population estimate as λ increases, as increasing values of λ place constraints on other parameters limiting overall uncertainty.

Lower percentiles of the population estimate were more stable (i.e. did not vary much) as a function of λ than upper percentiles. This is advantageous to *PBR* calculations, as it means that $N_{\min}$ is not very sensitive to the unknown growth rate. Further, estimates based on the alternative model (Equation 3.4) were very similar to those of the primary model (Equation 3.1). There was more uncertainty in N for the alternative model ($s_J = s$; Equation 3.4) as higher values of juvenile survival implied lower fecundity (for the same λ), increasing the possible combinations of b and k , especially for lower values of λ . However, the additional uncertainty was small enough that results are presented for the primary model only. For example, calculations of $N_{\min}$ for the two models for an albatross with $s = 0.96$, $\alpha = 10$, and $CV_{\hat{B}} = 0.5$ are within 5% of each other.

Simulations were fast (3 chains, 100,000 iterations/chain, <15s processing time on an AMD Athlon 64X2 Dual Core Processor 3800+, 2.01 GHz, 1 GB RAM) and model diagnostics were good (as would be expected for a model without data). A large number of iterations were necessary to produce confidence interval estimates with small levels of Monte Carlo error for a wide range of λ . In a setting where speed was important, fewer iterations could be used by restricting the range of λ and also by employing smoothers on parameter estimates as a function of λ .

3.6.1 Petrels

For a typical petrel species ($s = 0.93$ and $\alpha = 6$; Table A.1), the estimated population is $\hat{N} = 5.4$ (90% CI: 3.4 – 9.4× B) and $N_{\min} = 3.9 \times B$ when the population is stable (Table 3.1). When considering a variety of survival and age at first breeding rates, and considering $\lambda = 1 \pm 0.03$, the rule-of-thumb population multiplier ranges from about $5 \times B$ (90% CI: 3.4 – 7.1 × B) for a species that begins breeding at $\alpha = 5$ with survival $s = 0.90$, to $6 \times B$ (90% CI: 3.7 – 11.0 × B) for a species that begins breeding at $\alpha = 8$ with survival $s = 0.94$. A reasonable rule-of-thumb multiplier for $N_{\min}$ is $N_{\min} = 4 \times B$ for most situations when B is known (Table 3.1).

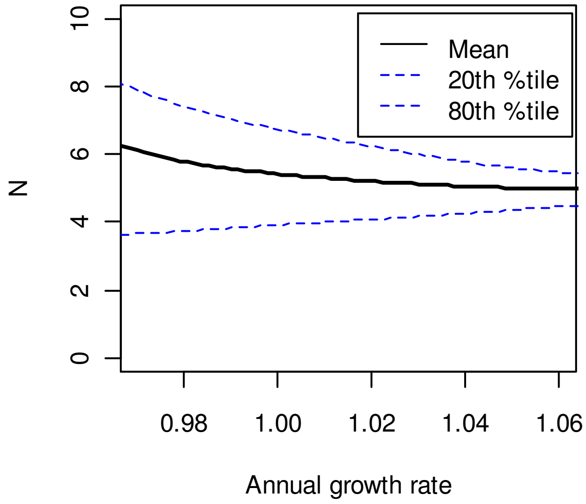

Figure 3.1. Population size of petrels per breeding pair as a function of λ (for a typical petrel species where $s = 0.93; \alpha = 6$).

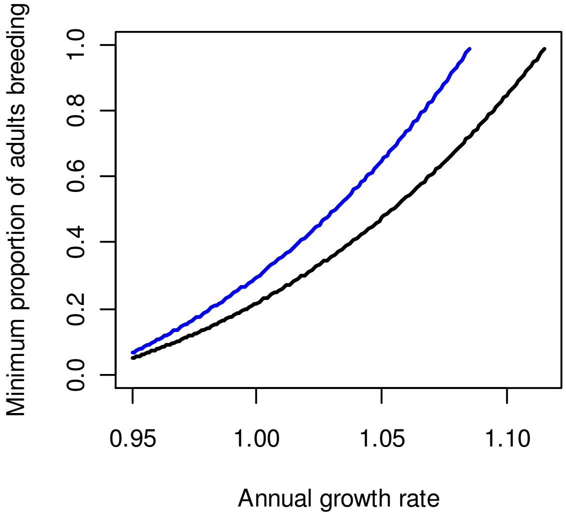

Figure 3.2. Minimum proportion of breeding adults for a typical petrel ($s = 0.93; \alpha = 6$) when $s_J = b = s$ (black line) and when $s_J = 0.9$ and $b = 0.8$ (blue line).

However, when uncertainty in the estimate of the number of breeding pairs is incorporated with uncertainty in the population multiplier, $N_{\min}$ can be considerably lower (Tables 3.2, 3.3, Figure 3.3). For example, for the typical petrel species described above, $N_{\min} = 2.8 \times B$ for a stable population when $CV_{\hat{B}} = 0.5$. Modifying the rule-of-thumb multiplier suggests that $N_{\min} = 4 \times B$ when B is known, $N_{\min} = 3.5 \times \hat{B}$ when $CV_{\hat{B}} = 0.25$, and $N_{\min} = 3 \times \hat{B}$ when $CV_{\hat{B}} = 0.5$.

While $N_{\min}$ varies considerably with λ for small coefficients of variation, as $CV_{\hat{B}}$ increases, $N_{\min}$ begins to stabilise across different values of λ (Figure 3.3). This suggests that the use of a constant rule-of-thumb multiplier is most appropriate for population estimates with high coefficients of variation, which conveniently are also likely to be populations where the least is known about λ.

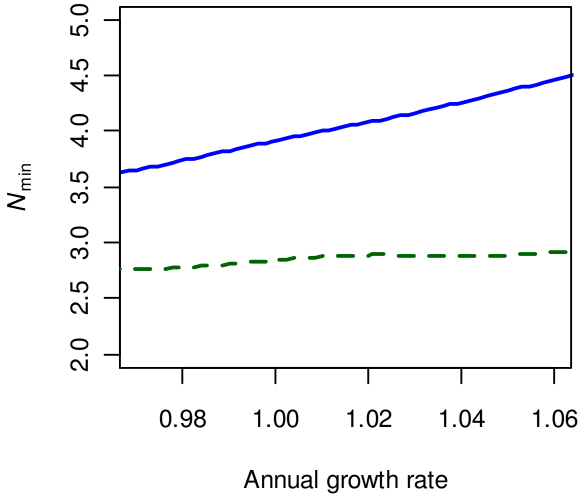

Figure 3.3. $N_{\min}$ per estimated breeding pair for a typical petrel ($s = 0.93; \alpha = 6$) as a function of λ when $CV_{\hat{B}} = 0$ (solid blue line) and $CV_{\hat{B}} = 0.5$ (dashed green line).

The rule-of-thumb multiplier for $N_{\min}$ still varies with s and α for large values of $CV_{\hat{B}}$. However, for $CV_{\hat{B}} = 0.5$, the observed variation for petrels is likely within about 10% of $N_{\min} = 3 \times \hat{B}$ (Table 3.3).

Finally, additional model constraints may be placed on population parameters. For example, it may be thought that juvenile survival is close to adult survival. This changes the nature of possible combinations of b and k at different values of λ (Figure 3.4). If juvenile survival is required to be high (e.g. $s_J > 0.9$), then bk is more constrained (Figure 3.4a) than if no additional constraints are placed on juvenile survival (Figure 3.4b). This highlights that the rule-of-thumb estimates presented are conditional on the population model used.

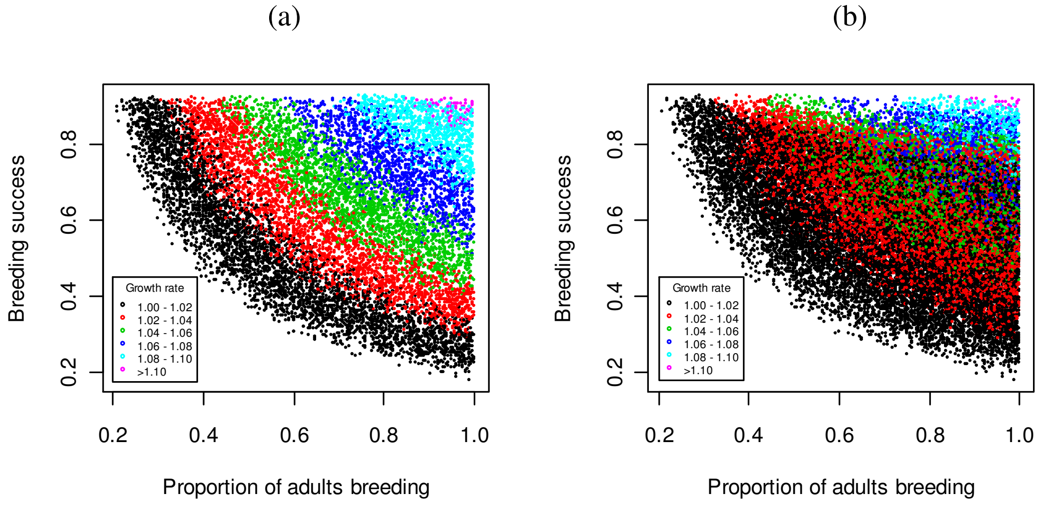
(a) (b)

Figure 3.4. Constraints between breeding success and the proportion of adults breeding amongst petrels for (a) high juvenile survival ($s_J > 0.9$) and (b) any juvenile survival for a typical petrel species ($s = 0.93; \alpha = 6$) versus annual growth rate for 30,000 simulations with $\lambda > 1$.

Table 3.1. Petrel population size (*N*) per breeding pair (B) for a stable ($\lambda = 1$), growing ($\lambda = 1.03$), and shrinking ($\lambda = 0.97$) population. Upper ($N_{0.95}$) and lower ($N_{0.05}$) limits from a 90% confidence interval, and 20th percentile estimates ($N_{\min}$), are included for the stable population.

		$\lambda = 1$				$\lambda = 1.03$		$\lambda = 0.97$	
s	α	N	$N_{\min}$	$N_{0.05}$	$N_{0.95}$	N	$N_{\min}$	N	$N_{\min}$
0.90	5	4.8	3.8	3.4	7.1	4.7	4.0	5.1	3.6
0.90	6	5.1	4.2	3.8	7.3	5.0	4.5	5.4	4.0
0.90	7	5.5	4.7	4.2	7.6	5.5	5.0	5.8	4.3
0.90	8	5.9	5.1	4.7	7.8	5.9	5.6	6.1	4.6
0.91	5	4.9	3.8	3.3	7.6	4.7	4.0	5.2	3.5
0.91	6	5.2	4.1	3.7	7.7	5.1	4.4	5.5	3.9
0.91	7	5.6	4.5	4.0	8.2	5.5	4.9	5.9	4.2
0.91	8	5.9	4.9	4.4	8.4	5.9	5.4	6.2	4.5
0.92	5	5.0	3.7	3.2	8.5	4.8	3.9	5.5	3.5
0.92	6	5.3	4.0	3.5	8.6	5.1	4.3	5.8	3.8
0.92	7	5.7	4.4	3.8	8.9	5.5	4.7	6.1	4.0
0.92	8	6.0	4.8	4.2	9.2	5.9	5.2	6.4	4.3
0.93	5	5.1	3.6	3.1	9.2	4.8	3.8	5.8	3.4
0.93	6	5.4	3.9	3.4	9.4	5.1	4.2	6.0	3.6
0.93	7	5.8	4.3	3.6	9.6	5.6	4.7	6.2	3.9
0.93	8	6.0	4.6	3.9	9.8	5.9	5.0	6.6	4.2
0.94	5	5.2	3.5	3.0	10.0	4.9	3.7	6.3	3.3
0.94	6	5.5	3.9	3.3	10.1	5.3	4.2	6.5	3.6
0.94	7	5.8	4.1	3.5	10.5	5.6	4.5	6.8	3.8
0.94	8	6.2	4.4	3.7	11.0	5.9	4.9	7.1	4.0

Table 3.2. Petrel population size (*N*) per observed breeding pair ($\hat{B}$) with $CV_{\hat{B}} = 0.25$ for a stable ($\lambda = 1$), growing ($\lambda = 1.03$), and shrinking ($\lambda = 0.97$) population. Upper ($N_{0.95}$) and lower ($N_{0.05}$) limits from a 90% confidence interval, and 20th percentile estimates ($N_{\min}$), are included for the stable population.

		$\lambda = 1$				$\lambda = 1.03$		$\lambda = 0.97$	
s	α	N	$N_{\min}$	$N_{0.05}$	$N_{0.95}$	N	$N_{\min}$	N	$N_{\min}$
0.90	5	4.8	3.4	2.7	8.1	4.7	3.5	5.1	3.3
0.90	6	5.2	3.7	3.0	8.3	5.0	3.8	5.4	3.6
0.90	7	5.6	4.1	3.3	8.8	5.5	4.2	5.8	3.9
0.90	8	5.9	4.4	3.5	9.2	5.9	4.6	6.1	4.2
0.91	5	4.9	3.4	2.6	8.5	4.7	3.5	5.2	3.2
0.91	6	5.2	3.7	2.9	8.6	5.1	3.9	5.5	3.5
0.91	7	5.6	4.0	3.1	9.2	5.5	4.2	5.9	3.8
0.91	8	5.9	4.3	3.4	9.5	5.9	4.6	6.2	4.0
0.92	5	5.0	3.3	2.5	9.2	4.8	3.5	5.5	3.2
0.92	6	5.3	3.6	2.8	9.3	5.1	3.8	5.8	3.5
0.92	7	5.7	3.9	3.0	9.8	5.5	4.1	6.1	3.7
0.92	8	6.0	4.2	3.3	10.3	5.9	4.4	6.4	4.0
0.93	5	5.1	3.3	2.5	9.7	4.8	3.4	5.8	3.2
0.93	6	5.4	3.5	2.7	10.1	5.1	3.7	6.0	3.3
0.93	7	5.8	3.8	2.9	10.3	5.6	4.1	6.2	3.6
0.93	8	6.1	4.1	3.1	10.7	5.9	4.4	6.6	3.8
0.94	5	5.2	3.2	2.4	10.5	4.8	3.3	6.3	3.1
0.94	6	5.5	3.5	2.6	10.7	5.3	3.7	6.5	3.3
0.94	7	5.8	3.7	2.8	11.3	5.5	4.0	6.8	3.5
0.94	8	6.2	4.0	3.1	11.8	5.9	4.4	7.1	3.7

Table 3.3. Petrel population size (*N*) per observed breeding pair ($\hat{B}$) with $CV_{\hat{B}} = 0.50$ for a stable ($\lambda = 1$), growing ($\lambda = 1.03$), and shrinking ($\lambda = 0.97$) population. Upper ($N_{0.95}$) and lower ($N_{0.05}$) limits from a 90% confidence interval, and 20th percentile estimates ($N_{\min}$), are included for the stable population.

		$\lambda = 1$				$\lambda = 1.03$		$\lambda = 0.97$	
s	α	N	$N_{\min}$	$N_{0.05}$	$N_{0.95}$	N	$N_{\min}$	N	$N_{\min}$
0.90	5	4.7	2.7	1.8	9.8	4.6	2.7	5.0	2.7
0.90	6	5.2	2.9	2.0	10.6	4.9	2.9	5.4	2.9
0.90	7	5.5	3.2	2.1	11.4	5.5	3.2	5.7	3.1
0.90	8	5.9	3.4	2.3	12.0	5.8	3.5	6.1	3.3
0.91	5	4.8	2.7	1.8	10.3	4.7	2.7	5.3	2.6
0.91	6	5.2	2.9	1.9	10.9	5.1	2.9	5.5	2.8
0.91	7	5.5	3.1	2.1	11.3	5.5	3.3	5.9	3.0
0.91	8	5.9	3.3	2.2	12.2	5.8	3.6	6.2	3.2
0.92	5	5.0	2.6	1.7	11.2	4.8	2.7	5.5	2.6
0.92	6	5.3	2.9	1.9	11.3	5.1	3.0	5.8	2.8
0.92	7	5.6	3.1	2.0	11.9	5.5	3.2	6.1	3.0
0.92	8	6.0	3.3	2.2	12.4	5.9	3.5	6.4	3.2
0.93	5	5.1	2.6	1.7	11.4	4.8	2.6	5.8	2.6
0.93	6	5.4	2.8	1.8	12.1	5.1	2.9	6.0	2.7
0.93	7	5.7	3.0	2.0	12.4	5.7	3.2	6.3	3.0
0.93	8	6.1	3.3	2.1	13.0	5.9	3.4	6.6	3.2
0.94	5	5.2	2.6	1.7	12.3	4.8	2.6	6.3	2.6
0.94	6	5.5	2.8	1.8	12.6	5.2	2.9	6.5	2.7
0.94	7	5.9	3.0	1.9	13.2	5.5	3.1	6.8	2.9
0.94	8	6.2	3.3	2.1	13.8	5.9	3.4	7.1	3.0

3.6.2 Biennially breeding albatrosses

Albatross populations may be supported by a relatively few number of breeding adults due to their high survival. For a typical albatross ($s = 0.96; \alpha = 10$, Table A.1) with biennial breeding, the estimated population is $\hat{N} = 12.6$ (90% CI: 5.5 – 22.4) and $N_{\min} = 7.8$ for each *per annum* breeding pair when the population is stable (Table 3.4). When uncertainty in the number of breeding pairs is considered, $N_{\min} = 7.3$ when $CV_{\hat{B}} = 0.25$, and $N_{\min} = 6.0$ when $CV_{\hat{B}} = 0.5$.

For the range of survival and age at first breeding rates that were considered, the rule-of-thumb population multiplier ranges from about $9 \times B$ for an early reproducing, low survival species to $17 \times B$ for a species that begins breeding at $\alpha = 12$ with survival $s = 0.97$ (although any species with such high survival rates are likely to be growing, not stable). A reasonable rule-of-thumb multiplier for $N_{\min}$ is $N_{\min} = 8 \times B$ when B is known and $N_{\min} = 6 \times \hat{B}$ for $CV_{\hat{B}} = 0.5$ for a stable population (Table 3.4); $N_{\min} = 7 \times \hat{B}$ is reasonable for $CV_{\hat{B}} = 0.25$. These values are also reasonable for populations in near optimal conditions (Table 3.5). For the scenarios with lower survival rates where a declining population is plausible, these multipliers are again reasonable.

Table 3.4. Albatross population size (*N*) per observed breeding pair ($\hat{B}$) for a stable population ($\lambda = 1$) with coefficient of variation $CV_{\hat{B}} = 0$ and $CV_{\hat{B}} = 0.5$, with 20th percentile estimates ($N_{\min}$), and limits from a 90% confidence interval ($N_{0.05}, N_{0.95}$).

		$CV = 0$				$CV = 0.5$		
s	α	N	$N_{\min}$	$N_{0.05}$	$N_{0.95}$	$N_{\min}$	$N_{0.05}$	$N_{0.95}$
0.94	8	9.2	6.8	5.4	14.1	4.9	3.1	19.5
0.94	10	9.9	7.5	5.9	14.5	5.4	3.5	20.8
0.94	12	10.4	8.3	6.7	14.8	5.8	3.8	21.0
0.95	8	10.3	6.9	5.2	17.2	5.1	3.2	23.4
0.95	10	10.8	7.5	5.7	17.6	5.5	3.5	23.4
0.95	12	11.3	8.2	6.3	17.7	5.9	3.7	24.7
0.96	8	12.1	7.2	5.0	22.2	5.6	3.3	28.4
0.96	10	12.6	7.8	5.5	22.4	6.0	3.5	29.2
0.96	12	13.1	8.4	6.1	22.7	6.4	3.9	29.3
0.97	8	15.9	8.2	5.2	32.1	6.5	3.6	39.5
0.97	10	16.4	8.7	5.7	32.5	6.9	3.8	40.5
0.97	12	16.6	9.2	6.1	32.4	7.2	4.0	40.3

Table 3.5. Maximum growth rates achievable for albatrosses from the matrix population model ($\lambda_{\max}$[MM]), and population size (*N* and 20th percentile estimates $N_{\min}$) per observed breeding pair ($\hat{B}$) for a population in near optimal conditions ($\lambda > \lambda_{\max}[\mathrm{MM}] - 0.015$) with coefficient of variation $CV_{\hat{B}} = 0$ and $CV_{\hat{B}} = 0.5$.

				$N_{\min}$	
s	α	$\lambda_{\max}$[MM]	N	$CV = 0$	$CV = 0.5$
0.94	8	1.05	8.2	7.8	5.2
0.94	10	1.04	9.2	8.4	5.5
0.94	12	1.03	10.1	9.1	5.8
0.95	8	1.06	8.2	7.7	4.8
0.95	10	1.05	9.2	8.4	5.6
0.95	12	1.04	10.2	9.5	6.0
0.96	8	1.07	8.1	7.6	4.9
0.96	10	1.06	9.2	8.4	5.3
0.96	12	1.05	10.1	9.4	5.9
0.97	8	1.08	8.3	7.8	5.0
0.97	10	1.07	9.2	8.7	5.5
0.97	12	1.06	10.1	9.4	5.9

3.7 Implications for management

In order to set mortality limits using the *PBR* method, estimates for $N_{\min}$ and $\lambda_{\max}$ are required. Combining the Niel and Lebreton (2005) estimate of $\lambda_{\max}$ with these estimates of $N_{\min}$ allows application of the PBR method for petrels and biennially breeding albatrosses based on the estimated number of breeding pairs and its coefficient of variation given λ, s, and α. This allows Equation 2.1 to be re-written as

$$PBR = \tau f \hat{B} \tag{3.11}$$

where τ is a coefficient that incorporates a species' maximum growth rate and a species-appropriate population multiplier, and also includes uncertainty in the estimate of the number of breeding pairs. Values for τ are presented in Table 3.6 for $\lambda \approx 1$. These values vary with λ, s, and α because the population multiplier does. However, they do not vary quickly, and these values should be appropriate for most situations in which management would consider applying the *PBR* method.

This suggests that, for a typical petrel species with $CV_{\hat{B}} = 0.5$, $PBR = 0.12 f \hat{B}$, while for a typical albatross species with $CV_{\hat{B}} = 0.5$, $PBR = 0.15 f \hat{B}$. Given $CV_{\hat{B}}$, τ varies considerably with s and α for petrels, but is relatively stable for albatrosses. In particular, low values of s lead to higher estimates of τ for petrels, which means that an underestimate of s (which should represent survival in optimal conditions) could potentially lead to too high of a PBR estimate.

The population estimates and rules-of-thumb are conditional on the model choice, so it is important to recognise model limitations. For example, the estimate of λ is relatively insensitive to k and b. Thus, even though k and b are likely to be stochastic (Chastel et al. 1995, Doherty et al. 2004), the estimate of λ will not change much. However, the census estimate is based only on the number of breeding birds, so does depend highly on k. Hence, it is best to use an average of several years' worth of census data (preferably from a time when all breeders could be observed), rather than just one census which may have been taken during a year with an unusually high or low level of breeding. More generally, the assumptions of constant parameter values over time and a stable age structure mean that estimates of N will be less accurate for populations undergoing rapid structural change (i.e. those that are out of equilibrium) than for those that are not. The sensitivities of these estimates to assumed parameter values could be assessed by considering a range of parameter values (as in Table 3.1).

One clear flaw in the population model is the assumption that all birds begin breeding at the same age. However, given that the rules-of-thumb do not differ greatly based on α, the simple population model with α equal to the mean age at first breeding should suffice. Further, while model assumptions about the structure of early age class survival have some impact on the population estimates, the impact is not substantial. This suggests that the population model used provides robust results even when α is not estimated well, especially when estimating $N_{\min}$ for use in the rule-of-thumb PBR equation.

This is a useful method for placing some bounds on the rule-of-thumb multipliers that could be used to estimate the population size of seabirds. The lack of constraints on k and b lead to wide bounds for the multipliers. However, providing more constraints would mean that the ratio of unaccounted error (i.e. bias due to population simplifications such as assuming a constant α and ignoring temporal variations) to accounted error would grow. It is proposed as a tool when little data are available, but should make way to other methods when more data are available.

Table 3.6. Coefficient (τ; Equation 3.11) to use in *PBR* calculations for petrels and albatrosses given s, α, $\hat{B}$, and $CV_{\hat{B}}$ for a stable population ($\lambda \approx 1$).

			$CV = 0$		$CV = 0.5$	
s	α	$\lambda_{\max}$[DIM]	$N_{\min}$	τ	$N_{\min}$	τ
Petrels						
0.90	5	1.12	3.8	0.22	2.7	0.16
0.90	6	1.10	4.2	0.21	2.9	0.14
0.90	7	1.09	4.7	0.21	3.2	0.14
0.90	8	1.08	5.1	0.20	3.4	0.14
0.91	5	1.11	3.8	0.21	2.7	0.15
0.91	6	1.10	4.1	0.20	2.9	0.14
0.91	7	1.09	4.5	0.19	3.1	0.13
0.91	8	1.08	4.9	0.19	3.3	0.13
0.92	5	1.11	3.7	0.20	2.6	0.14
0.92	6	1.09	4.0	0.18	2.9	0.13
0.92	7	1.08	4.4	0.18	3.1	0.13
0.92	8	1.07	4.8	0.18	3.3	0.12
0.93	5	1.10	3.6	0.18	2.6	0.13
0.93	6	1.09	3.9	0.17	2.8	0.12
0.93	7	1.08	4.3	0.17	3.0	0.12
0.93	8	1.07	4.6	0.16	3.3	0.12
0.94	5	1.09	3.5	0.17	2.6	0.12
0.94	6	1.08	3.9	0.16	2.8	0.12
0.94	7	1.07	4.1	0.15	3.0	0.11
0.94	8	1.07	4.4	0.15	3.3	0.11
Albatrosses						
0.94	8	1.07	6.8	0.23	4.9	0.16
0.94	10	1.06	7.5	0.21	5.4	0.15
0.94	12	1.05	8.3	0.21	5.8	0.14
0.95	8	1.06	6.9	0.22	5.1	0.16
0.95	10	1.05	7.5	0.20	5.5	0.15
0.95	12	1.05	8.2	0.19	5.9	0.14
0.96	8	1.06	7.2	0.21	5.6	0.16
0.96	10	1.05	7.8	0.19	6.0	0.15
0.96	12	1.04	8.4	0.18	6.4	0.14
0.97	8	1.05	8.2	0.21	6.5	0.17
0.97	10	1.04	8.7	0.19	6.9	0.15
0.97	12	1.04	9.2	0.18	7.2	0.14

3.8 WinBUGS code for Chapter 3

The WinBUGS model for petrels is:

```
model {
  surv.j ~ dunif(0, surv.a)
  lambda ~ dunif(lambda.lb, lambda.ub)

  # Nuisance k, b determine fecundity
  k ~ dunif(0,1)
  b ~ dunif(0,surv.j)
  fec <- k*b/2

  # Numerical method for constraining to characteristic equation
  zero.hat <-  pow(lambda, alpha - 1)*(surv.a - lambda) +
         pow(surv.j, alpha - 1) *k* b/2
  zero.l <- zero.hat - delta
  zero.u <- zero.hat + delta
  zero ~ dunif(zero.l, zero.u)

  # Calculate the population size multiplier per BP
  BP.perBP <- 1
  a.alpha.perBP <- 2*BP.perBP*(1 - surv.a/lambda)/k
  NB.perBP <- 2*BP.perBP*(1 - k)/k
   for (i in 1:(alpha-1)) {
     juv.term[i] <- pow(lambda/surv.j, i)
  }
  JUV.perBP <- a.alpha.perBP*sum(juv.term[])
  N.perBP <- 2*BP.perBP + NB.perBP + JUV.perBP
  N.adults.perBP <- 2*BP.perBP + NB.perBP

  # Calculate the actual population estimate given BP.hat, CV.BP, and
  # N.perBP; see Wade 1998, Equation 3, re-arranging terms
  Zp ~ dnorm(0,1)
  BP <- exp(log(BP.hat/sqrt(1+CV.BP*CV.BP)) + Zp*sqrt(log(1+CV.BP*CV.BP)))
  JUV <- JUV.perBP*BP
  N <- N.perBP*BP
  N.adults <- N.adults.perBP*BP
 }
```

The WinBUGS model for albatrosses is:

```
model {
  surv.j ~ dunif(0, surv.a)
  lambda ~ dunif(lambda.lb, lambda.ub)

  # Nuisance parameters b, eta, k determine fecundity;
  # k is constrained because successful breeders become obligate non-breeders
  b ~ dunif(0,surv.j)
  eta ~ dunif(0,10000)
  k <- 1/(1 + b + eta)
  fec <- k*b/2

  # Numerical method for constraining to characteristic equation
  zero.hat <-  pow(lambda, alpha - 1)*(surv.a - lambda) +
        pow(surv.j, alpha - 1) *k* b/2
  zero.l <- zero.hat - delta
  zero.u <- zero.hat + delta
  zero ~ dunif(zero.l, zero.u)

  # Calculate the population size multiplier per BP
  BP.perBP <- 1
  a.alpha.perBP <- 2*BP.perBP*(1 - surv.a/lambda)/k
  NB.perBP <- 2*BP.perBP*(1 - k)/k
   for (i in 1:(alpha-1)) {
     juv.term[i] <- pow(lambda/surv.j, i)
  }
  JUV.perBP <- a.alpha.perBP*sum(juv.term[])
  N.perBP <- 2*BP.perBP + NB.perBP + JUV.perBP
  N.adults.perBP <- 2*BP.perBP + NB.perBP

  # Calculate the actual population estimate given BP.hat, CV.BP, and
  # N.perBP; see Wade 1998, Equation 3, re-arranging terms
  Zp ~ dnorm(0,1)
  BP <- exp(log(BP.hat/sqrt(1+CV.BP*CV.BP)) + Zp*sqrt(log(1+CV.BP*CV.BP)))
  JUV <- JUV.perBP*BP
  N <- N.perBP*BP
  N.adults <- N.adults.perBP*BP
 }
```

3.9 References for Chapter 3

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Chapter 4. Estimating generation time for populations with age-specific fecundities and unknown juvenile survival

In age-classified population models where all the parameters are known, the generation time and growth rate may be calculated in a straightforward manner. For many populations, some parameters, such as juvenile survival, are difficult to estimate accurately. For populations where all animals begin breeding at the same age with constant fecundity, generation time and maximum growth rate may be calculated knowing only age at first reproduction and adult survival (Niel and Lebreton 2005, Chapter 2). This result is extended to populations with age-specific fecundities but unknown juvenile survival, using six bird species as examples. If age-specific fecundities were unknown for these species, a constant-fecundity model with an ad hoc adjustment to age at first breeding provides similar estimates of generation time and maximum growth rate.

Population models where all animals begin breeding at the same age are useful as long as the consequences of this simplification are understood. A more realistic model for many species is to allow age-specific fecundities, accounting for animals beginning to breed at different ages. Generation time is an important population parameter (Sarich and Wilson 1973, Martin and Palumbi 1993, Lebreton and Clobert 1993, Gaillard et al. 2005, Gillooly et al. 2005, Lebreton 2005, Niel and Lebreton 2005), and failure to account for age-specific fecundities may lead to substantial bias in its estimation. However, the estimate of generation time is also dependent on adult survival (s) and the growth rate (λ), and bias in the estimate of either of these can lead to even greater bias in the estimate of generation time.

Niel and Lebreton (2005) and Gaillard et al. (2005) presented an estimate of generation time based only on age at first breeding, adult survival, and population growth rate, assuming fecundity and survival are constant from the onset of breeding. That is, in addition to assuming that all individuals within an age class behave similarly, it is assumed that all mature age classes are equivalent. Importantly, estimates of juvenile survival – often difficult to estimate – are not present in the calculation of generation time.

For many species (such as albatrosses and petrels), fecundity increases over a number of years (Schwarz and Arnason 2000), in contrast the assumption that mature age classes have constant fecundity in Niel and Lebreton (2005) and Gaillard et al. (2005). A more realistic model for many species still assumes that individuals within an age class behave similarly, but allows fecundity to vary between age classes. The calculation of generation time for such a model is derived. Similar to the formula from Lebreton (2005) and Gaillard et al. (2005), juvenile survival is not present in the calculation of generation time. Further, survival from birth to the age of first breeding may also be calculated. Finally, a modification to the formula for the maximum growth rate for a bird species (Niel and Lebreton 2005) is presented.

4.1 Introduction

Age-classified matrix models may be constructed to study a population when age-specific breeding and survival rates are available (Leslie 1945, Caswell 2001). One key area of study is the sensitivity of the population growth rate to the different demographic parameters in the model (Caswell 2001). Generation time is related to the sensitivity of a population to changes in adult survival or fecundity (Lebreton and

Clobert 1993, Gaillard et al. 2005, Lebreton 2005). In addition to studying sensitivities, generation time is an important metric in other contexts. For example, the intrinsic maximum growth rate per generation is approximately constant (Fowler 1988, Niel and Lebreton 2005), and generation time is also of interest in the study of evolution rates (Sarich and Wilson 1973, Martin and Palumbi 1993, Gillooly et al. 2005).

Various definitions of generation time exist (Leslie 1966, Caswell 2001, Niel and Lebreton 2005). The mean generation length of a population is defined as

$$\bar{T} = \sum_{i=1}^{\infty} i l_i f_i \lambda^{-i} \tag{4.1}$$

where $l_i = \prod_{j=1}^{i} s_j$ is the survival from birth to age *i*, s_i is the survival from age $i-1$ to i, f_i is the annual fecundity at age *i* (mean number of young), and λ is the annual (or other appropriate time unit) growth rate of the population (Leslie 1966, Niel and Lebreton 2005, Gaillard et al. 2005). In this context, fecundity equals the proportion of animals in each age class breeding times breeding success (live birth), times the number of young; s_1 is the survival rate from birth to age 1. Mean generation length was chosen as a suitable measure of generation time as it is insensitive to senescence (Niel and Lebreton 2005), which is not accounted for in most population models.

Niel and Lebreton (2005) used allometric relationships to estimate the optimal generation time ($\bar{T}_{op} = \bar{T}$ when conditions are optimal) and maximum growth rate ($\lambda_{\max}$), given only adult survival (s) and age at first breeding (α). In non-optimal situations, they provided an estimate of generation time given α, s, and the growth rate (λ). Their results were based on a population model in which all animals have constant fecundity from age α, zero fecundity prior to α, and constant survival s for some age $i \le \alpha$ (hereafter, the *constant-fecundity model*). Further, they assumed $\lambda > s$, which must always occur under optimal conditions for any viable species (otherwise $\lambda_{\max} < 1$ and the species would not exist) and would generally be true even in non-optimal situations. These assumptions lead to the relationship

$$\bar{T} = \alpha + \frac{s}{\lambda - s} \tag{4.2}$$

while allometric relationships lead to the approximation

$$\bar{T}_{op} \ln \lambda_{\max} \approx a_r a_T \tag{4.3}$$

where a_r and a_T are allometric coefficients associated with body weight and generation time. Hence, under ideal conditions,

$$\lambda_{\max} \approx \exp\left[a_r a_T \left(\alpha + \frac{s}{\lambda_{\max} - s} \right)^{-1} \right] \tag{4.4}$$

which can be easily solved using iterative methods. Niel and Lebreton (2005) then studied populations of 13 bird species undergoing optimal or near optimal growth, and estimated that, for bird species, $a_r a_T \approx 1$ (asymmetric 95% CI: 0.98 - 1.15). Maximum growth rates based on allometric relationships were compared to estimates from matrix model methods (Caswell 2001), and they found that that there was a high level of correlation between the two estimates ($R = 0.88$, excluding two Passerine species, and based on additional approximations).

While Niel and Lebreton's (2005) results are mathematically elegant, the assumption of constant fecundity across age classes may not hold in practice. Of the 13 species used in their paper, demographic data for 6 species (Table 4.1) does not support the constant fecundity assumption. Instead, while survival is constant (or nearly constant) prior to first breeding, fecundity increases over a number of age classes. Thus, a more realistic model – the *varying-fecundity model* – assumes constant survival from the first age class with non-zero fecundity (β), but allows fecundity to increase over a number of age classes, becoming constant at some later age (γ). The constant-fecundity model, with a fixed age at first breeding α, and the varying-fecundity model are equivalent if $\alpha = \beta = \gamma$.

Equation 4.1 may be used to estimate generation time even when the constant fecundity assumption fails to hold, with

$$\hat{\bar{T}} = \hat{\alpha} + \frac{s}{\lambda - s} \tag{4.5}$$

A naive estimator using Equation 4.5 based on $\hat{\alpha} = \beta$ can result in substantial bias compared to Equation 4.1; for the six species with varying fecundity, the magnitude of the bias was greater than one year for two species (Table 4.2). However, if relative fecundities are known, Equation 4.2 may be modified and an exact calculation of $\bar{T}$ is still possible. If relative fecundities are unknown but still thought to increase with age, an ad hoc adjustment may be reasonable, with $\hat{\alpha} = \beta + \varepsilon$ for some ε.

4.2 Methods

The estimate of generation time presented by Niel and Lebreton (2005) and Gaillard et al. (2005) is derived from the definition of mean generation length ($\bar{T}$; Equation 4.1) and the Euler-Lotka equation

$$1 = \sum_{i=1}^{\infty} l_i f_i \lambda^{-i} \tag{4.6}$$

A similar approach to theirs may be used to calculate the generation time for the varying-fecundity model. In the constant-fecundity model, the assumption of constant fecundity and adult survival means that $f_i = f$ and $s_i = s$ for $i \geq \alpha$; $f_i = 0$ for $i < \alpha$; and $l_i = l_\alpha s^{i-\alpha}$ for $i \geq \alpha$. For the varying-fecundity model, the assumptions around fecundity are relaxed to allow breeding to begin at age β, becoming constant by age γ. That is, $f_i = f$ for $i \geq \gamma$, $f_i = 0$ for $i < \beta$, and $0 < f_i \leq f$ for $\beta \leq i \leq \gamma$, and survival (s) is assumed to be constant from at least age β, so $l_i = l_\beta s^{i-\beta}$ for $i \geq \beta$. In general, $\beta < \gamma$, but this definition allows the constant-fecundity model to be contained within the set of all varying-fecundity models, with $\beta = \gamma = \alpha$. Further, relative fecundities are defined as $k_i = f_i / f$.

Table 4.1. Demographic parameters and matrix model estimates of the mean generation time ($\bar{T}$) and annual growth rate (λ) for six bird populations where fecundity increases over several age classes (data from Niel and Lebreton 2005).

Species		β	γ	s	$k_\beta, \ldots, k_{\gamma-1}$	$\bar{T}$	λ
Black-legged kittiwake	*Rissa tridactyla*	5	6	0.90	0.90	9.177	1.120
Snow goose	*Anser caerulescens*	2	4	0.83	0.41, 0.91	5.014	1.167
Barnacle goose	*Branta leucopsis*	3	4	0.95	0.50	7.498	1.184
Great cormorant	*Phalacracorax carbo*	2	8	0.90	0.26, 0.47, 0.72, 0.91, 0.97, 0.99	6.283	1.185
Black-headed gull	*Larus ridibundus*	2	3	0.90	0.43	6.291	1.138
White stork	*Ciconia ciconia*	2	4	0.78	0.16, 0.40	4.981	1.210

4.2.1 Calculating generation time

Thus, for the varying-fecundity model,

$$
\begin{aligned}
\bar{T} &= \frac{fl_\beta}{\lambda^\beta}\sum_{i=\beta}^{\infty} ik_i s^{i-\beta}\lambda^{\beta-i} \\
&= \frac{fl_\beta}{\lambda^\beta}\left(\sum_{i=\beta}^{\infty}(i-\beta)\left(\frac{s}{\lambda}\right)^{i-\beta} + \sum_{i=\beta}^{\infty}\beta\left(\frac{s}{\lambda}\right)^{i-\beta} + \sum_{i=\beta}^{\gamma-1} i\left(1-k_i\right)\left(\frac{s}{\lambda}\right)^{i-\beta}\right)
\end{aligned}
$$

The two infinite series have well known solutions (i.e. see Purcell and Varberg 1987, or other elementary calculus texts) for $s/\lambda < 1$, and the equation above reduces to

$$\bar{T} = \frac{fl_\beta}{\lambda^\beta}\left[\left(1-{}^{s}\!/\!_{\lambda}\right)^{-1}\left(\beta+\frac{s}{\lambda-s}\right)-\sum_{i=\beta}^{\gamma-1} i\left(1-k_i\right)\left(\frac{s}{\lambda}\right)^{i-\beta}\right] \tag{4.7}$$

In a similar manner, the Euler-Lotka equation reduces to

$$1 = \frac{fl_\beta}{\lambda^\beta}\left[\left(1-{}^{s}\!/\!_{\lambda}\right)^{-1}-\sum_{i=\beta}^{\gamma-1}\left(1-k_i\right)\left(\frac{s}{\lambda}\right)^{i-\beta}\right] \tag{4.8}$$

Solving Equation 4.8 for fl_β/λ^β and substituting into Equation 4.7 yields the desired result,

$$\bar{T} = \frac{\beta+\dfrac{s}{\lambda-s}-\left(1-{}^{s}\!/\!_{\lambda}\right)\displaystyle\sum_{i=\beta}^{\gamma-1} i\left(1-k_i\right)\left(\frac{s}{\lambda}\right)^{i-\beta}}{1-\left(1-{}^{s}\!/\!_{\lambda}\right)\displaystyle\sum_{i=\beta}^{\gamma-1}\left(1-k_i\right)\left(\frac{s}{\lambda}\right)^{i-\beta}} \tag{4.9}$$

While Equation 4.9 is not as elegant as Equation 4.2, it has the similar benefit of not requiring parameter estimates for pre-breeders, which are often difficult to estimate (Schwarz and Arnason 2000). In particular, pre-breeding survival rates may be difficult to estimate, as juvenile age classes may not be present (as is the case for many seabirds), and juvenile survival and emigration rates are typically confounded.

The other demographic parameters may be estimated using capture-recapture techniques, and λ may also be estimated from census data. When the constant-fecundity model is valid (i.e. $\beta = \gamma = \alpha$), Equation 4.9 reduces to Equation 4.2.

4.2.2 Estimating $\lambda_{\max}$

For species in ideal conditions, Equations 4.3 and 4.9 are combined to estimate $\lambda_{\max}$ as

$$\lambda_{\max} \approx \exp\left[a_r a_T \frac{1-\left(1-{}^{s}\!\big/\!{}_{\lambda_{\max}}\right)\sum_{i=\beta}^{\gamma-1}\left(1-k_i\right)\left(\frac{s}{\lambda_{\max}}\right)^{i-\beta}}{\beta+\frac{s}{\lambda_{\max}-s}-\left(1-{}^{s}\!\big/\!{}_{\lambda_{\max}}\right)\sum_{i=\beta}^{\gamma-1} i\left(1-k_i\right)\left(\frac{s}{\lambda_{\max}}\right)^{i-\beta}} \right] \tag{4.10}$$

A species' annual growth potential ($R_{\max} = \lambda_{\max} - 1$) may be used in calculations of harvest limits and rates (Wade 1998, Taylor 2000, Niel and Lebreton 2005, Chapter 2). The percentage bias in $R_{\max}$ directly translates into a proportional bias in harvest rate (Chapter 2). This suggests that a useful measure of different estimates of $\lambda_{\max}$ is

$$\pi = \left(\hat{R}_{\max} - R_{\max}\right)\Big/R_{\max} \tag{4.11}$$

where positive values of π would translate into the proportional overharvest compared to the desired harvest.

4.3 Bias in generation time and $\lambda_{\max}$ caused by use of the constant-fecundity model

For the six bird species where fecundity increases over a number of age classes, three approaches to estimating $\bar{T}$ and $\lambda_{\max}$ are considered. The first approach (the naive approach) assumes constant fecundity with $\hat{\alpha} = \beta$ used to estimate $\lambda_{\max}$ and $\bar{T}$ from Equations 4.4 and 4.5. The second approach again uses the constant-fecundity model (Equations 4.4 and 4.5), but uses an ad hoc adjustment of $\hat{\alpha} = \beta + \varepsilon$, where $\varepsilon = \min\left[1, (\beta + \gamma)/2\right]$ was chosen as a reasonable but arbitrary adjustment (i.e. add half a year if $\gamma = \beta + 1$ and a whole year otherwise). A less arbitrary adjustment may be mean age at first breeding (Schwarz and Arnason 2000, Schwarz and Stobo 2000), but data was unavailable for these species. The third approach uses the varying-fecundity model (Equations 4.9 and 4.10) to estimate $\bar{T}$ and $\lambda_{\max}$; the calculation of $\bar{T}$ will be exact (if the parameter values are exact) for all species except for great cormorant (*Phalacracorax carbo*) where survival rates continued to vary after the onset of breeding (Niel and Lebreton 2005). The bias in the estimate of $\bar{T}$ and $\lambda_{\max}$ is assessed, as well as π (the proportional bias in $R_{\max}$), for the different approaches.

For species with varying-fecundity, use of the constant-fecundity model results in substantial bias in the estimate of generation time (Table 4.2). The naive estimate ($\hat{\alpha} = \beta$) results in a mean underestimate of generation time of 0.7 years ($\hat{\sigma} = 0.4$) for the six species studied. The ad hoc adjustment performs somewhat better, with a mean absolute bias of 0.2 years ($\hat{\sigma} = 0.2$) for the six species. The varying-fecundity model is exact for five of the species; for the great cormorant there is a small bias (0.02) in the estimate of generation time.

All six species studied were bird species in optimal or near optimal conditions, so the approximation from Equation 4.10 was used to estimate $\lambda_{\max}$ and the proportional overharvest $\pi = \left(\hat{R}_{\max} - R_{\max}\right) / R_{\max}$ (Table 4.3), where $R_{\max}$ is based on the matrix model estimates (Table 4.1). Differences in π due to the estimation method (and controlling for species) were estimated using a two-way ANOVA with Tukey's adjustment for multiple comparisons (Rice 1995); 95% confidence intervals for each comparison were equal to the observed difference ± 0.20. The naive estimate performs worse than either of the other two approaches, with a mean overestimate for $R_{\max}$ of $\pi = 0.36$. The other two approaches perform similarly to each other, with $\pi = 0.05$ for the ad hoc adjustment to the constant-fecundity model, and $\pi = 0.08$ for the varying-fecundity model.

Table 4.2. Bias in the estimate of mean generation time from the naive constant-fecundity model ($\hat{\alpha} = \beta$), and the adjusted constant-fecundity model ($\hat{\alpha} = \beta + \min\left[1, (\beta + \gamma)/2\right]$), by using Equation 4.5, versus using the varying-fecundity model (Equation 4.9).

		Model	
Species	*naive*	*adjusted*	*varying*
Black-legged kittiwake	-0.08	0.42	na
Snow goose	-0.55	0.45	na
Barnacle goose	-0.45	0.06	na
Great cormorant	-1.18	-0.18	0.02
Black-headed gull	-0.51	-0.01	na
White stork	-1.17	-0.17	na
Mean bias	-0.66	0.09	na

Table 4.3. Matrix model and allometric-based estimates of $\lambda_{\max}$ ($\lambda_{\max}[\mathrm{MM}]$, $\lambda_{\max}[\mathrm{DIM}]$) for the naive constant-fecundity model ($\hat{\alpha} = \beta$; Equation 4.4), the adjusted constant-fecundity model ($\hat{\alpha} = \beta + \min\left[1, (\beta + \gamma)/2\right]$; Equation 4.4), and the varying-fecundity model (Equation 4.10). The resulting proportional overharvest (π; Equation 4.11) from each allometric estimate is compared to the matrix model estimate.

		$\lambda_{\max}$ [DIM]			π		
Species	$\lambda_{\max}$ [MM]	*naive*	*adjusted*	*varying*	*naive*	*adjusted*	*varying*
Black-legged kittiwake	1.12	1.12	1.11	1.11	-0.04	-0.11	-0.05
Snow goose	1.17	1.31	1.21	1.25	0.83	0.28	0.49
Barnacle goose	1.18	1.13	1.11	1.11	-0.31	-0.39	-0.38
Great cormorant	1.18	1.24	1.17	1.16	0.32	-0.06	-0.11
Black-headed gull	1.14	1.24	1.20	1.20	0.74	0.44	0.44
White stork	1.21	1.34	1.24	1.23	0.64	0.13	0.08

The six species studied were also used by Niel and Lebreton (2005) to develop the approximation $\bar{T}_{op} \ln \lambda_{\max} \approx 1$; thus, the same species were used to develop methods and then test them for bias. However, the level of approximation used (i.e. 1 represents a convenient value between 0.98 and 1.15) should alleviate any problems that this may cause. Further, the primary conclusion – that the naive estimate is not very good – is intuitively correct. In the constant-fecundity model, an underestimate of the age at first breeding results in an overestimate of $\lambda_{\max}$. By using the naive estimate with the constant-fecundity model when the varying-fecundity model is correct, in essence the age at first breeding is underestimated and a positive bias in $\lambda_{\max}$ could be expected.

4.3.1 Sensitivity of generation time and maximum growth rate to parameter estimates compared to model-based bias

Estimates of age at first reproduction, adult survival, and the growth rate are required to estimate generation time even for the simplest calculations of generation time (i.e. Equation 4.2). If no estimates are available and values arbitrarily chosen, then substantial bias in the estimate of generation time may result. For the constant-fecundity model, age at first reproduction and adult survival are required to estimate the maximum growth rate. For this model, underestimates of age at first reproduction or survival lead to overestimates in $\lambda_{\max}$; short and moderately-lived species growth rates are sensitive to α, while adult survival is more important for longer-lived species (Chapter 2).

A hypothetical bird species with a medium-length lifespan may have $\alpha = 3$, $s = 0.8$, $\lambda = 1.1$, and $\bar{T} = 5.7$ (Equation 4.2). Similar species such as the snow goose or white stork show that use of the naive estimator when there is variable fecundity can produce bias in excess of ±0.5 years in the estimate of $\bar{T}$ (Table 4.2) and more than ±0.05 years^{-1} in the estimate of $\lambda_{\max}$ (Tables 4.1, 4.3), potentially leading to substantial overharvest ($\pi > 0.25$, Table 4.3).

To achieve a similar level of bias in $\bar{T}$, bias in s or λ on the order of ±0.05 would be necessary; to achieve bias in excess of ±0.05 years^{-1} in the estimate of $\lambda_{\max}$, the bias in s would need to be in excess of ±0.10. Thus, if this species was better described by the variable-fecundity model and the naive estimator was used, bias in the estimates of generation time and maximum growth rate caused by use of the constant-fecundity model may be substantially greater than error related to parameter estimation. For these species, the impact of the population model on the estimate of generation time can be substantial and should not be ignored.

The results are somewhat different for a hypothetical, long-lived species (such as albatrosses) which may have $\alpha = 10$, $s = 0.96$, and $\lambda = 1.02$, and $\bar{T} = 26$ (Equation 4.2). If there is a +0.01 bias in either s or a -0.01 bias in λ, then $\hat{\bar{T}}$ will be biased by 3.4 years (bias in s) or 3.2 years (bias in λ). The large change in generation time for a small change in s or λ is because $\partial\bar{T}/\partial s = \lambda/(\lambda - s)^2$ and $\partial\bar{T}/\partial\lambda = -s/(\lambda - s)^2$, so error in either s or λ will have a large impact on $\bar{T}$ if s and λ are close to each other, as would be expected for long-lived species. Translating this into potential overharvest, $\hat{s} = s - 0.04$ results in a 25% increase in the estimate of $R_{\max}$.

If the species was better described by the variable-fecundity model, where some birds begin breeding at age 8 and all birds are adults by age 12 with $(k_8, ..., k_{12}) = (0.2, 0.4, 0.6, 0.8, 1)$, then the generation time is $\bar{T} = 25.9$ (Equation 4.9). The naive estimator ($\hat{\alpha} = 8$; $\bar{T} = 24$, Equation 4.5) would then have a bias of -2 years, and the ad hoc estimator ($\hat{\alpha} = 9$; $\bar{T} = 25$, Equation 4.5) would have a bias of -1 years. In this example, use of the naive estimator translates into a 15% increase in the estimate of $R_{\max}$ compared to the varying-fecundity estimate, and the ad hoc adjustment translates into a 6% increase. Hence, while the impact of using the naive or ad hoc estimators to calculate generation time and $\lambda_{\max}$ is not trivial, parameter errors may have substantially more effect on the estimate of generation time and $\lambda_{\max}$ for long-lived species.

4.4 Discussion

When the constant-fecundity assumption is invalid, substantial underestimation (>1 year) in the estimate of generation time calculated from Equation 4.5 may occur if β is used as the age at first breeding. If the relative fecundities are known, it is possible to calculate generation time using Equation 4.9. If the relative fecundities are unknown, using Equation 4.9 is not an option, and using an ad hoc adjustment to α could be valuable. The ad hoc approach chosen here – add half a year if β and γ differ by only a year, and a whole year otherwise – worked reasonably well for these species; another likely choice would be mean age at first breeding. For long-lived species, the level of bias due to the constant-fecundity population model may be small compared to potential bias due to λ or s. However, the effort required to implement Equations 4.5, 4.9, or 4.10 is small. For moderately-lived species, model choice may have a greater effect and should not be ignored. Further, using an ad hoc adjustment as in Equation 4.5 should suffice when relative fecundities are unknown.

The allometric relationship developed by Niel and Lebreton (2005) may be used with the alternate estimators of generation time to estimate $\lambda_{\max}$ for bird populations. However, in the approximation $\bar{T}_{op} \ln \lambda_{\max} \approx 1$, the right-hand side was chosen from an estimated range (0.98, 1.15) for the sake of simplicity (Niel and Lebreton 2005), and there would be additional variation beyond that for an individual population. However, there still appears to be a benefit from using either an ad hoc adjustment to the age at first breeding in Equation 4.4 or the varying-fecundity model (Equation 4.10) compared to the naive estimator.

As would be expected, use of a more realistic population model results in more accurate calculations. In general, these results suggest that a simple population model with an ad hoc adjustment to age at first breeding is nearly as good. However, for species with varying fecundity rates, using the earliest age that *some* birds begin breeding as an estimate of the age that *all* birds begin breeding can result in substantial bias in the estimates of generation time and maximum growth rate. Ultimately, this could lead to substantial overharvest of a species if the maximum growth rate is used to set mortality limits.

4.5 References for Chapter 4

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Chapter 5. Estimating age at first breeding for Gibson's albatrosses using capture-recapture data

The age at first breeding (α_B) is an important demographic parameter in determining maximum growth rate (Chapter 2), population size (Chapter 3), and generation time (Chapter 4). After adult survival, it is one of the most important parameters in describing the population dynamics of albatrosses and other Procellariiformes, and a key parameter in calculating the potential biological removal (*PBR*; see Chapter 2) of birds. Albatrosses do not begin breeding for many years (Table A.1), with some first breeding in their teens. This means that even long-term studies of birds banded as chicks may not last long enough to observe the entire process of recruitment to breeding. Estimates based only on observations (naive estimates) may be biased by imperfect observation, emigration, and study length, and modelling approaches should be used to estimate the mean age at first breeding ($E(\alpha_B)$). Because breeding albatrosses are easily detected, most of the difficulties with estimating age at first breeding are related to emigration and study length, rather than capture probabilities. While the effect of imperfect capture probabilities on recruitment is well understood, the use of naive estimates for albatrosses could be tempting because breeding birds are easily observed.

This chapter is concerned with data where there is one study area, birds are banded as chicks and as adults, but age is known only for birds banded as chicks. Some of these chicks will emigrate away from the study area, while birds from outside of the study area may immigrate to it. The emigration could be due to natal dispersal (recruiting to another colony), or to philopatric birds returning outside a limited study area. The age of the immigrants is unknown, so the only birds available to estimate age at first breeding are those that are banded as chicks *and* return to the study area to breed. Because immigrants breed at an older age than non-immigrants (Frederiksen and Bregnballe 2001), estimates of age at first breeding based only on birds banded as chicks will be negatively biased. Further, when the study duration is limited, extrapolation based on a parametric model may be required, making the model choice important but possibly untestable.

Existing capture-recapture methods are available to estimate local recruitment; i.e. the age at first breeding for those chicks that will breed in the study area (Lebreton et al. 1990, Clobert et al. 1994, Pradel 1996, Pradel et al. 1997, Pradel and Lebreton 1999, Schwarz and Arneson 2000), with some extension possible when there are multiple sites (Lebreton and Pradel 2002, Lebreton et al. 2003, Hénaux et al. 2007) or other auxiliary information is available. Note that reverse-time models that condition on observed recruitment (Pradel 1996, Pradel et al. 1997) become naive estimates when the capture probability is 1. While they address bias related to an imperfect observation process, bias due to emigration and study length remain. Typically, these local age-specific breeding rates are estimated because confounding between other states leads to parameter redundancy (e.g. it is impossible to distinguish between birds outside of the study area, breeding or not, and a dead bird). Here, a multistate model is used to model recruitment to the breeding population for known-age birds banded as chicks, observed at one location. Parameter redundancy is addressed by making assumptions about survival that allow estimation of emigration rates.

In this chapter, problems with the naive estimate are discussed, showing the possible large negative bias caused by limited study length and emigration. However, appropriate modelling combined with additional model assumptions can alleviate the bias when the additional assumptions are correct. Simulated capture-recapture datasets are generated from such a model, and model-based estimates of the mean age at first reproduction are compared to analytic calculations. Finally, data for Gibson's albatrosses (*Diomedea gibsoni*; also listed as *D. antipodensis gibsoni* as per Burg and Croxall 2004) is used as a real example with more complex models. In the interest of consistency and brevity, real data and simulated data are both for biennially-breeding birds, such as those in genus *Diomedea*; however, many of the results would be the same or similar for other Procellariiformes.

Data was provided by K. Walker and G. Elliott (New Zealand Department of Conservation) for $N = 1246$ Gibson's albatrosses banded as chicks beginning in 1993 (but only 4 were banded prior to 1995; Table 5.1), with data collected through 2006. However, only 42 Gibson's albatrosses were observed breeding. With limited data, model assumptions about recruitment to breeding play an additional role in the estimate of $E(\alpha_B)$. In particular, the function chosen for recruitment to breeding for older age classes can not be compared to data. Three recruitment functions are compared to determine the sensitivity of the estimated mean age at first breeding to the assumed functional form.

5.1 Life-cycle stages

The population structure of Procellariiformes may be reasonably described by a stage by age-based population model (Lebreton 2005) with three stages. After fledging, birds leave the colony and do not return for a multi-year period, which is termed the *juvenile* stage, beginning at age 1. Birds recruit to the colony as *pre-breeders* over a period of several years, with some birds recruiting earlier and some recruiting later. After a period of prospecting often lasting several years, *pre-breeders* become *adults*, which incorporate several breeding states. In this chapter, it is assumed that there is at least one year of prospecting prior to breeding. It is expected that a proportion of the birds will emigrate from the birth site prior to breeding, but that emigration will be low after the onset of breeding (as in Lebreton et al. 2003).

Biennial breeders (Diomedea)

Albatrosses in *Diomedea* raise one chick at a time, and successful breeders do not breed the following year (except in unusual circumstances). This leads to three different adult states. *Successful breeders* become *obligate non-breeders* the following year. *Failed breeders* may or may not breed again the following year. In addition to *obligate non-breeders*, there are *other non-breeders*, which are those birds that could potentially breed (i.e. were not s*uccessful breeders* the prior year) but do not. The *other non-breeders* could be further classified as birds that are in the breeding population but are skipping a year (*skippers*) or birds that are not part of the breeding population (*long-term non-breeders*); in this context, the adult stage could be thought of as two distinct stages, comprising those birds that sometimes breed and those birds that do not.

5.2 Age at first return and breeding

The expected or mean age at first return and breeding for those birds that will eventually return or breed are defined as

$$E\left(\alpha_R\right) = \sum_{i=1}^{\infty} i\pi_R^{(i)} \Big/ \sum_{i=1}^{\infty} \pi_R^{(i)} \tag{5.1}$$

and

$$E\left(\alpha_B\right) = \sum_{i=1}^{\infty} i\pi_B^{(i)} \Big/ \sum_{i=1}^{\infty} \pi_B^{(i)} \tag{5.2}$$

respectively, where $\pi_R^{(i)}$ is the probability that a bird returns to a colony at age *i*, and $\pi_B^{(i)}$ is the probability that a bird first breeds at age *i*. The probabilities that a bird first returns or breeds at age *i* amongst those that eventually return or breed are

$$\Pr\left(\alpha_R = i\right) = \pi_R^{(i)} \Big/ \sum_{j=1}^{\infty} \pi_R^{(j)} \tag{5.3}$$

and

$$\Pr\left(\alpha_B = i\right) = \pi_B^{(i)} \Big/ \sum_{j=1}^{\infty} \pi_B^{(j)} \tag{5.4}$$

The denominators in Equations 5.1 and 5.2 represent the proportion of banded chicks that will eventually return ($\sum_{j=1}^{\infty} \pi_R^{(j)}$) or breed ($\sum_{j=1}^{\infty} \pi_B^{(j)}$) in any location. However, in most studies, death and emigration are confounded, which may make it impossible to get unbiased estimates of $\pi_R^{(i)}$ and $\pi_B^{(i)}$.

5.2.1 Naive estimates

A simple approach to estimating the mean age at first return ($\bar{\alpha}_R^{(N)}$) and first breeding ($\bar{\alpha}_B^{(N)}$) is to examine the birds that have been observed returning or breeding, and to calculate naive estimates,

$$\bar{\alpha}_R^{(N)} = \sum_{i=1}^{T} i N_i^{(R)} \Big/ \sum_{i=1}^{T} N_i^{(R)} \tag{5.5}$$

and

$$\bar{\alpha}_B^{(N)} = \sum_{i=1}^{T} i N_i^{(B)} \bigg/ \sum_{i=1}^{T} N_i^{(B)} \tag{5.6}$$

where $N_i^{(R)}$ is the number of birds observed returning to the study area and $N_i^{(B)}$ is the number of birds observed breeding in the study area at age *i*, and *T* is the age of the oldest birds in the study.

The capture probability for non-breeding birds that are present in the study area may be low in many years, while the limited study duration means that birds likely to begin breeding at a younger age are more likely to be observed breeding than those that will begin breeding at a later age. This means that $\bar{\alpha}_R^{(N)}$ is likely to be positively biased due to the imperfect capture probability, partially offset by a negative bias from the limited study period, while $\bar{\alpha}_B^{(N)}$ may be positively or negatively biased, depending on capture probabilities, emigration rates, and study duration. Capture-recapture methods combined with appropriate population models that incorporate capture probabilities, study duration, and emigration may be used to avoid the bias.

5.2.2 The effect of emigration

Imperfect capture probabilities clearly result in positive biases in estimates of age at first return and breeding, and data truncation due to a limited study duration clearly causes negative bias. The effect of unmodelled emigration is less obvious; depending on how it occurs, it may cause no bias, positive bias, or negative bias. Emigration may occur at any stage, but juvenile emigration and pre-breeder emigration are the primary concerns for estimating age at first return and breeding.

Age at first return

The probability that a bird returns to a colony at age *i* is a combination of surviving to age *i* ($l_i = \prod_{k=1}^{i} s_k$ where s_k is annual survival from age $k-1$ to k), not returning prior to age *i*, and finally returning at age *i* given survival and not returning earlier ($\psi_R^{(i)}$), or

$$\pi_R^{(i)} = \begin{cases} l_{k_R} \psi_R^{(k_R)} & \text{if } i = k_R \\ l_i \psi_R^{(i)} \prod_{k=k_R}^{i-1} \left(1 - \psi_R^{(k)}\right) & \text{if } i > k_R \end{cases} \tag{5.7}$$

where k_R is the earliest age at which birds return. Unmodelled emigration will then cause a negative bias in $\pi_R^{(i)}$. If the probability that a juvenile bird will emigrate from the study area (and not returning to the study area as a pre-breeder first) equals ε_J, then apparent survival to age *i* is $l_i^A = l_i \left(1 - \varepsilon_J\right)$. In this case, use of apparent survival instead of actual survival causes no bias in Equation 5.1, as $1 - \varepsilon_J$ may be factored out of both the numerator and denominator in Equation 5.1 when Equation 5.7 is used for $\psi_R^{(i)}$. Hence, juvenile emigration of this form does not affect the mean age at first return (as in Lebreton et al. 1990).

If the probability that juveniles emigrate depend on the age that they will return to a colony, then $l_i^A = l_i \left(1 - \varepsilon_J^{(i)}\right)$, and $1 - \varepsilon_J^{(i)}$ does not factor out in Equation 5.1. In this case, the mean age at first return will be biased. The direction of bias would depend on whether emigration was more likely for early-returning birds (positive bias) or late-returning birds (negative bias). An example of this is when there is a yearly probability of emigration; then the longer that a bird takes to return, the more likely it is to emigrate.

Age at first breeding

It was assumed that birds return at least one year prior to breeding, so the probability of breeding at age *i* is a combination of returning at age $j < i$, surviving as a pre-breeder from age *j* to *i* ($l_{i|j}$), not breeding prior to age *i*, and finally breeding at age *i* given survival and not breeding earlier ($\psi_B^{(i)}$). Hence, for $i > k_R$,

$$\pi_B^{(i)} = \sum_{j=k_R}^{i-1} \Pr\left(\alpha_R = j\right)\left[\pi_B^{(i)} \mid \alpha_R = j\right] = \sum_{j=k_R}^{i-1} \Pr\left(\alpha_R = j\right) l_{i|j} \psi_B^{(i)} \prod_{k=j}^{i-1}\left(1-\psi_B^{(k)}\right) \qquad (5.8)$$

Similar to age at first return, if the probability of emigration out of the study area (given recruitment to the study area) is a fixed value for all birds (ε_P), then the use of apparent survival ($l_{i|j}^A = l_{i|j}\left(1-\varepsilon_P\right)$) versus actual survival will result in an unbiased estimate of age at first breeding, assuming juvenile emigration is also fixed. However, this may be biologically implausible. While it may be reasonable to assume that chicks have a fixed probability of returning to their natal area given survival, pre-breeders who have returned to their natal area may be more likely to emigrate the longer they are unable to secure a mate (as in Jenouvrier et al. 2008). In this case, birds that will breed at a later age will emigrate at a higher rate, and the estimated age at first breeding will be negatively biased unless emigration is accounted for.

Recommendations for incorporating emigration in a population model

If emigration occurs, it either needs to be well-behaved, or there needs to be a way to separate survival and emigration rates. Separating survival and emigration at the juvenile stage is especially difficult. This suggests making the additional model assumption that the probability of juvenile emigration is ε_J. If the probability of emigration is a constant value for all juvenile birds (rather than a yearly rate or age-specific probability), then bias in the age at first breeding may be avoided. For pre-breeders, it may be reasonable to assume that the underlying survival probability (s_P) is the same as for adults, and that the observed differences are due to annual emigration (ε_P). Further, for birds with high nest-fidelity, there will be minimal emigration after breeding begins, and it should be possible to calculate an estimate of adult survival (s) that is minimally affected by emigration. This suggests the following:

(1) Assume a fixed level of juvenile emigration, so that apparent juvenile survival to age k_R is $l_{k_R}^A = l_{k_R}(1-\varepsilon_J)$; if this assumption is valid, then $E(\alpha_R)$ and $\Pr(\alpha_R = i)$ are unbiased. Further, assume that the underlying annual survival rate for birds aged $i > k_R$ equals adult survival s; this assumption is not strictly necessary for juveniles, but in practice, this or a similar constraint provides more realistic survival estimates;

(2) Model separate pre-breeder and adult survival rates to account for annual emigration during pre-breeder stages, and assume that the difference is the emigration rate, so $s_P = s - \varepsilon_P$ and $l_{i|j}^A = l_{i|j}(1-\varepsilon_P)^{i-j}$;

(3) In Equation 5.8, calculate $\pi_i^{(B)}$ using the estimated adult survival rate in place of the pre-breeder survival rate to avoid the bias due to emigration (i.e. $\hat{l}_{i|j} = \hat{l}_{i|j}^A \big/ (1-\hat{\varepsilon}_P)^{i-j}$ where $\hat{\varepsilon}_P = \hat{s} - \hat{s}_P$);

(4) Use the values from (3) and Equation 5.2 to estimate $E(\alpha_B)$.

5.3 Simple example

The bias of the naive estimator depends on survival and capture probabilities, emigration, and the study duration, as well as the age-specific probability of breeding for the first time. For purposes of illustration, consider a simple example where observation of breeding birds is perfect, no birds breed prior to age β, all surviving and non-emigrating birds return prior to age β, survival (s) is constant from age β, and the probability that a surviving, non-breeding bird age $a \geq \beta$ breeds for the first time (ψ_B) is constant. Further, assume that the probability that a juvenile emigrates is ε_J, while pre-breeders have yearly emigration rate ε_P. The assumption that ψ_B is constant is chosen for mathematical simplicity and implies that the mode of the distribution of age at first breeding equals β; in the analysis of real data a more complex function is probably warranted. With these model assumptions, for $i \geq \beta$, Equation 5.8 reduces to

$$\pi_B^{(i)} = l_\beta s^{i-\beta} (1-\psi_B)^{i-\beta} \psi_B$$

The mean age at first breeding may be simplified to

$$E(\alpha_B) = \beta + \frac{r}{1-r} \tag{5.9}$$

by using geometric series, noting that $\sum_{i=1}^{\infty} i\pi_B^{(i)} = l_\beta \psi_B \left[r/(1-r)^2 + \beta/(1-r) \right]$, and $\sum_{i=1}^{\infty} \pi_B^{(i)} = l_\beta \psi_B/(1-r)$, where $r = s(1-\psi_B)$.

5.3.1 Bias due to the limited study period

If the naive estimator is used instead, with the population followed for $T \geq 0$ years beyond age β, then

$$E\left(\bar{\alpha}_B^{(N)}\right) = \left(1-r^{T+1}\right)^{-1}\left\{\beta + \frac{r}{1-r} - r^{T+1}\left(\beta + T + 1 + \frac{r}{1-r}\right)\right\} \tag{5.10}$$

noting that

$\sum_{i=1}^{\beta+T} i\pi_B^{(i)} = l_\beta \psi_B \left\{ r\big/(1-r)^2 + \beta\big/(1-r) - r^{T+1}\left[r\big/(1-r)^2 + (\beta+T+1)/(1-r) \right]\right\}$ and $\sum_{i=1}^{\beta+T} \pi_B^{(i)} = l_\beta \psi_B \big/ (1-r) \cdot \left(1-r^{T+1}\right)$. The bias of the naive estimator for this simple example may be calculated by combining Equations 5.9 and 5.10, or by a graphical display as in Figure 5.1. Depending on the underlying population structure, substantial bias can remain even for birds followed for many years after initial breeding.

5.3.2 Bias due to emigration

It was assumed that there are two sources of emigration, that juvenile emigration is a fixed value ε_J (so apparent survival to age β is $l_\beta^A = l_\beta\left(1-\varepsilon_J\right)$), and that pre-breeder emigration occurs at yearly rate ε_P. As noted in Section 5.2.2, this form of juvenile emigration will not effect the estimated age at first return or breeding. However, if the existence of pre-breeder emigration is ignored, then survival will be negatively biased, with the amount of bias depending on how many breeding adults are included when estimating s. In order to account for emigration during the pre-breeding phase, a reasonable approach to modelling this data would be to estimate separate pre-breeder and breeder survival rates. If the estimate of pre-breeder survival ($s_P = s - \varepsilon_P$) is used as the survival estimate in Equation 5.9, then the mean age at first breeding that incorporates emigration ($E^{(\varepsilon)}\left(\alpha_B\right)$) will be a negatively biased estimate of $E\left(\alpha_B\right)$, i.e.,

$$E^{(\varepsilon)}\left(\alpha_B\right)=\beta+\frac{\left(s-\varepsilon_P\right)\left(1-\psi_B\right)}{1-\left(s-\varepsilon_P\right)\left(1-\psi_B\right)}<E\left(\alpha_B\right) \tag{5.11}$$

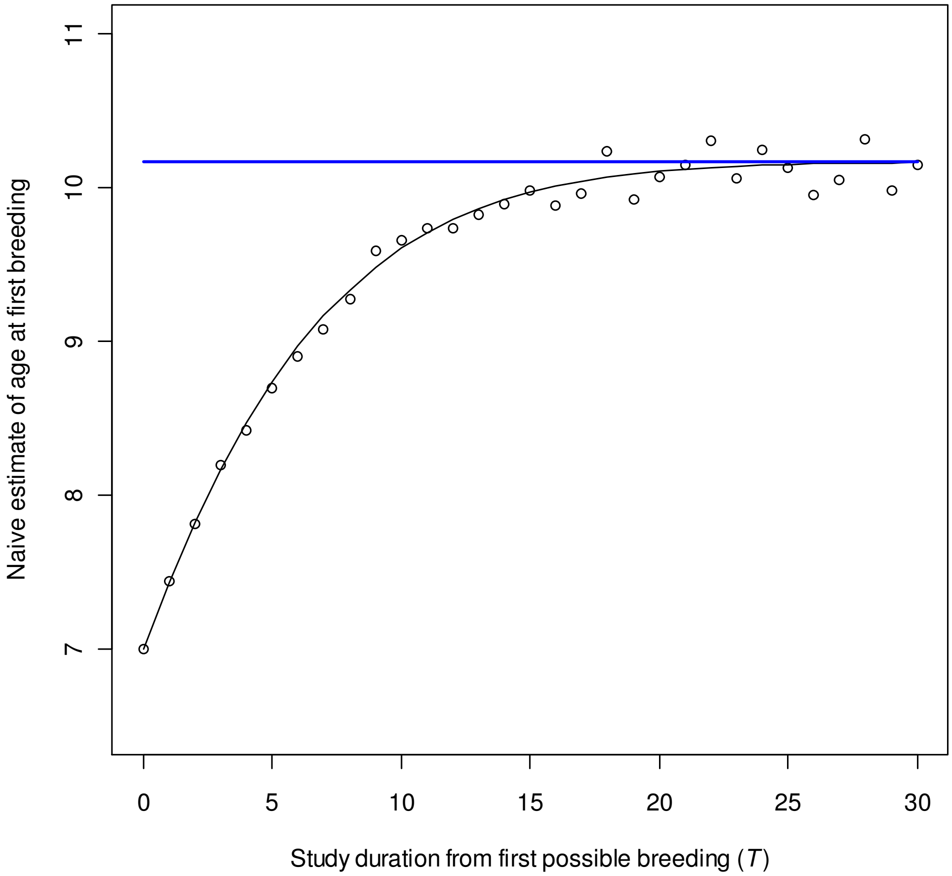

Figure 5.1. Estimated age at first reproduction (black line) using the naive estimator (Equation 5.6) for birds followed T years beyond the first age at which some birds reproduce ($\beta=7$). Observation of breeding birds was assumed to be perfect, no birds breed prior to age β, survival ($s=0.95$) is constant from age $a\geq\beta$, and the probability that a surviving, non-breeding bird age $a\geq\beta$ breeds for the first time was $\psi_B=0.2$. The true age at first reproduction is given by the blue line, while the points are based on simulations of 1000 living birds aged $\beta-1$.

5.4 Modelling approach using capture-recapture data

The estimated mean age at first breeding ($\bar{\alpha}_B$) will be biased if the naive estimator ($\bar{\alpha}_B^{(N)}$) is used. Instead, a model-based approach that accounts for the limited study duration, emigration, and the imperfect observation process should be used to estimate the age at first breeding. However, in many practical cases, limited data may be available to select an appropriate population model, and the model used may have a substantial effect on $\bar{\alpha}_B$ and the distribution of α_B. In these circumstances, it is important to determine the sensitivity of the estimated age at first breeding to different models.

Data for these species generally comprises two types of information: capture data (was a previously banded bird observed in a given year or not) and state data (i.e. was the bird observed breeding or in some other state) for each banded bird, each year. In some cases, other data may also be available, such as recovery of dead birds or knowledge of breeding success (*b*). Since birds are not always re-sighted (for example, at-sea juveniles have a re-sighting probability of 0, while obligate non-breeders often have very low re-sighting probabilities), in many years the state is unknown and must be estimated.

Multi-state capture-recapture methods (Brownie et al. 1993) may be employed for this data. These methods allow the estimation of survival probabilities (*s*; these may also depend on other covariates, such as year or gender), transition probabilities (ψ) between different states given survival, and re-sighting probabilities (*p*). One approach to analysing this data is to treat unobserved states (as well as other latent variables) as missing values that require estimation, which naturally lends itself to a Markov-chain Monte Carlo (MCMC) approach (Dupuis 1995).

For these analyses, birds are classified as belonging to one of five possible states (breeder (1), obligate non-breeder (2), other non-breeder/pre-breeder (3), juvenile (4), or dead (5)). Other non-breeders and pre-breeders are combined into one observable state (i.e. they are indistinguishable to an observer), separated by an unobserved latent variable ($I = 1$ if the bird has ever bred, 0 otherwise). The probability of moving from one state to another is described by a transition probability matrix (*TPM*), where transition probabilities may depend on covariates such as age, gender, or year. The *i*, *j*th entry of the *TPM* represents the probability of moving from state *i* in year *t* to state *j* in year *t* + 1.

When there are competing models, various information criterion exist (AIC, BIC, QAIC, DIC) exist that require calculation of the deviance for model comparison or calculation of model weights. State and capture data can be used to calculate the deviance, $D = -2\log L$, where the likelihood, conditional on the initial states, is calculated as

$$L = \prod_{i=1}^{B} \prod_{t_{i+1}}^{T} \psi_{S_{i,t-1},S_{i,t}} \left(p_{S_{i,t}} C_{i,t} + \left(1 - p_{S_{i,t}}\right)\left(1 - C_{i,t}\right)\right)$$

where

B is the number of birds in the study,

T is the length of the study,

t_i is the year the *i*th bird was banded,

$S_{i,t}$ is the state of the *i*th bird in the *t*th year (observed or unobserved),

$\psi_{S_{i,t-1},S_{i,t}}$ is the probability of transitioning from $S_{i,t-1}$ to $S_{i,t}$,

$p_{S_{i,t}}$ is the probability of observing state $S_{i,t}$,

$C_{i,t}$ is an indicator variable equal to 1 if the *i*th bird is observed in the *t*th year, and 0 otherwise.

5.5 Simulated data

Capture-recapture data for albatrosses was simulated and a Bayesian capture-recapture model was fitted to measure any bias in the estimated mean age at first breeding or other model parameters due to emigration and study duration, when the generating and estimating model agree. This simulation study reflects the type of data that may be available for a study of albatrosses, although simplified to some extent for illustrative purposes. An important aspect of the simulated data is that capture probabilities of breeding birds was high (0.95), reflecting a situation where the naive estimate of age at first breeding could be expected to perform reasonably well.

Data were simulated for 500 birds banded as chicks and 500 birds banded as breeding adults, with the study duration equal to 12 years. Simulations were computer intensive, limiting the practical number of replicates that could be used to estimate the bias for the *k*th parameter (B_{ζ_k}). The number of simulations ($R = 25$) was designed to achieve a standard error in $\hat{B}_{\bar{\alpha}_B}$ of approximately 0.1, based on a standard error of approximately 0.5 from one initial simulation, with estimates from each simulation combined to estimate

$$\hat{B}_{\zeta_k} = \frac{1}{25}\sum_{r=1}^{25}\hat{\zeta}_{k,r} - \zeta_k \tag{5.12}$$

where ζ_k is the *k*th parameter and $\hat{\zeta}_{k,r}$ is its estimate from the *r*th simulation; *t*-based confidence intervals were constructed. Bias in the estimated mean age at first breeding was of primary interest, but other parameters were monitored as well. Analyses were run using the OpenBUGS variant (Thomas et al. 2006, version 3.0.3) of BUGS (Bayesian analysis using Gibbs sampling, Lunn et al. 2000), with additional analyses performed in R (R Development Core Team 2008, version 2.7.0) using the R2WinBUGS library (Sturtz et al. 2005).

Parameter values were similar to those obtained in the analyses of Gibson's albatrosses and Antipodean albatrosses (*Diomedea antipodensis*) (Fletcher et al. 2008), except in those analyses the estimated survival rates for juveniles and pre-breeders were confounded with emigration, and a different model was used for recruitment to breeding. For the simulated data, survival from banding to age 2 was $s_2 = 0.90$, assuming banding occurred near age 1 prior to leaving the colony (otherwise, this would be $l_2 = 0.90$). Although banding may occur earlier, it is assumed that banded chicks who die prior to leaving the colony would be recorded as a failed breeding attempt, so the chicks will have effectively reached age 1. Survival from age 2 was $s = 0.95$. The probability that a bird banded as a chick would emigrate prior to returning to the colony (given survival) was $\varepsilon_J = 0.2$, so apparent survival from banding to returning to the colony at age *i* was $l_i^A = l_2^A s^{i-2} = \left(1-\varepsilon_J\right) s_2 s^{i-2}$. Pre-breeders had an annual emigration rate of $\varepsilon_P = 0.05$, so apparent pre-breeder survival was $s_P = s - \varepsilon_P = 0.90$. Age-specific recruitment probability to the colony was given by a logistic function, $\operatorname{logit}\left(\psi_R^{(a)}\right) = \beta_0 + \beta_1 a$ with $\beta_0 = -2.5$ and $\beta_1 = 1$ for birds aged $a \geq 3$, with $\psi_R^{(a)} = 0$ otherwise. The probability that a living pre-breeder aged $a \geq 8$ breeds for the first time was assumed to be a constant value; the age-specific probability of breeding for the first time was

$\psi_B^{(a)} = 0.1$ for $a \geq 8$ and $\psi_B^{(a)} = 0$ otherwise.

Adult birds (i.e. those that have already bred) had parameter values $b = 0.6$, $v = 0.6$, $\psi_{2,1} = 0.8$, and $\psi_{3,1}^{(A)} = 0.5$, where, given survival,

> b is breeding success (the probability of a surviving adult successfully raising a chick to age 1),
> v is the probability that a failed breeder attempts to breed the following year,
> $\psi_{2,1}$ is the probability an obligate non-breeder attempts to breed the following year, and
> $\psi_{3,1}^{(A)}$ is the probability an adult other non-breeder attempts to breed the following year.

It was assumed that at-sea juveniles, obligate non-breeders, dead birds, and birds that have emigrated could not be re-sighted. Among living birds that have not emigrated, breeding adults had re-sighting probability $p_1 = 0.95$, non-breeding adults had re-sighting probability $p_3^{(I=1)} = 0.6$, and pre-breeders had re-sighting probability $p_3^{(I=0)} = 0.2$. Further, it was assumed that an observer could not distinguish between a pre-breeder and an adult non-breeder, but that adult breeders could be correctly identified. Thus, the breeding status of a bird (which is unknown) determines transition probabilities, and this latent variable must also be estimated during the modelling process.

Observations of birds depend on emigration in addition to their actual states. For example, in order for a bird to have any chance of being observed in state (1), it must be breeding *and* not have emigrated. The 'local survival' *TPM* then depends on breeding status and age with apparent survival rates adjusted for emigration, so

$$TPM^{(a,I)} = \begin{pmatrix} (1-b)\,v\,s & b\,s & (1-b)(1-v)\,s & 0 & 1-s \\ \psi_{2,1}\,s & 0 & \left(1-\psi_{2,1}\right)s & 0 & 1-s \\ \psi_{3,1}^{(a+1,I)}\,s_3^{(I)} & 0 & \left(1-\psi_{3,1}^{(a+1,I)}\right)s_3^{(I)} & 0 & 1-s_3^{(I)} \\ 0 & 0 & \psi_R^{(a+1)}\,s_J^{(a+1)} & \left(1-\psi_R^{(a+1)}\right)s_J^{(a+1)} & 1-s_J^{(a+1)} \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix} \qquad (5.13)$$

where

> I is a breeding status indicator variable, equal to 1 for adults, 0 otherwise,
>
> $s_3^{(I=1)} = s$ and $s_3^{(I=0)} = s - \varepsilon_P$,
>
> $s_J^{(2)} = s_2\left(1-\varepsilon_J\right)$ and $s_J^{(a)} = s$ for $a > 2$; and
>
> $\psi_{3,1}^{(a,I=1)} = \psi_{3,1}^{(A)}$ for all a, and $\psi_{3,1}^{(a,I=0)} = \psi_B^{(a)}$.

Although the *TPM* is based on local survival (and s_2 and ε_J are confounded), emigration is suitably well-behaved and good estimates of $E\left(\alpha_R\right)$ and $E\left(\alpha_B\right)$ should still be obtainable. After each set of state and capture data was simulated, a Bayesian capture-recapture model was fitted based on the *TPM* in Equation 5.13. Hence, for the *i*th bird, the state of the bird in the *t*th year (S_t) follows a categorical distribution with probabilities given by the row corresponding to the prior year's state, breeding status, and age, i.e.

$$S_t \sim \text{Categorical}\left(TPM_{S_{t-1},\cdot}^{(a_{t-1},I_{t-1})}\right)$$

while the capture data (C_t) follows a Bernoulli distribution with the probability determined by the current year's state and breeding status, i.e.

$$C_t \sim \text{Bernoulli}\left(p_{S_t}^{(I_t)}\right)$$

Uniform(0,1) priors were used for all transition parameters and non-zero capture probabilities, except the following:

$\varepsilon_P \sim \text{Uniform}(0, s)$,

$\beta_0 \sim \text{Normal}(0, \sigma = 10)$, and

$\beta_1 \sim \text{Normal}(0, \sigma = 10 \mid \beta_1 > 0)$ (i.e. from a truncated-Normal distribution)

5.5.1 Population projections from simplified models

In addition to estimating age at first breeding, the *TPM* can be modified for matrix model population projections and estimations of asymptotic growth rates and other derived parameters (Caswell 2001). The projection matrix $\boldsymbol{\psi}$ is formed by combining age- and state-specific fecundity with the transpose of TPM, with entries corresponding to the death state removed (Lebreton 2005). Entries in *TPM* may also be modified to adjust for emigration or immigration. Combined with the number of living birds of age *a* in state *i* during the *t*th year ($x_{i,t}^{(a)}$) and the overall age-by-state vector for year *t* ($\mathbf{x}_t^{(a)} = \begin{bmatrix} x_{1,t}^{(a)} & x_{2,t}^{(a)} & x_{3,t}^{(a)} & x_{4,t}^{(a)} \end{bmatrix}^T$), the expected number of birds of age $a+1$ in each state the following year is $\mathbf{x}_{t+1}^{(a+1)} = \boldsymbol{\psi}\mathbf{x}_t^{(a)}$. Further, the full projection matrix may be used to estimate a simpler, age-based projection matrix, $\boldsymbol{\psi}_a$.

Given survival and transition estimates, it is straightforward to calculate the proportion of birds of each age class in each state, and therefore the proportion breeding, and ultimately the age-specific fecundity rate ($f^{(a)}$). In this context, age-specific fecundity is the expected number of chicks surviving to age 1 per bird age of a. Assuming a stable population structure, it may be calculated from an initial number of juveniles, $x_4^{(1)}$. This is projected forwards where the number of 2-year-old juveniles the next year is,

$$x_4^{(2)} = s_2 x_4^{(1)},$$

while, for older age classes, the number of juveniles is based on those surviving and not returning to the colony, i.e.

$$x_4^{(a)} = sx_4^{(a-1)}\left(1-\psi_R^{(a)}\right).$$

The number of pre-breeders is comprised of recently returned juveniles and pre-breeders that do not become breeders, so

$$x_3^{(a,I=0)} = s\left(x_4^{(a-1)}\psi_R^{(a)} + x_3^{(a-1,I=0)}\left(1-\psi_B^{(a)}\right)\right).$$

For adults, the number of breeders is composed of new breeders, last year's failed breeders attempting to breed again, last year's obligate non-breeders returning to breed, and other non-breeders returning to breed, so

$$x_1^{(a)} = s\left(\psi_B^{(a)} x_3^{(a-1,I=0)} + x_1^{(a-1)}\left(1-b\right)v + x_2^{(a-1)}\psi_{2,1} + x_3^{(a-1,I=1)}\psi_{3,1}^{(A)}\right).$$

Similarly, the number of obligate non-breeders is

$$x_2^{(a)} = sx_1^{(a-1)}b,$$

and the number of other non-breeders is

$$x_3^{(a)} = s\left(x_1^{(a-1)}\left(1-b\right)\left(1-v\right) + x_2^{(a-1)}\left(1-\psi_{2,1}\right) + x_3^{(a-1,I=1)}\left(1-\psi_{3,1}^{(A)}\right)\right).$$

The proportion of birds of each age-class that are breeding is $k^{(a)} = x_1^{(a)} \big/ x^{(a)}$ and age-specific fecundity is $f^{(a)} = bx_1^{(a)} \big/ \left(2x^{(a)}\right)$, where $x^{(a)} = \left|\mathbf{x}^{(a)}\right|$. Emigration- and immigration-adjusted survival rates are needed in order to make projections for an entire population. If $k^{(a)} \approx k^{(a+1)}\ \forall a \geq n$, and $n = 10$ (say), the age-adjusted projection matrix is

$$\boldsymbol{\psi}_a = \begin{bmatrix} 0 & 0 & \cdots & 0 & f^{(8)} & f^{(9)} & f^{(10+)} \\ l_2 & 0 & \ddots & 0 & 0 & 0 & 0 \\ 0 & s & \ddots & 0 & 0 & 0 & 0 \\ 0 & 0 & \ddots & 0 & 0 & 0 & 0 \\ 0 & 0 & \ddots & s & 0 & 0 & 0 \\ 0 & 0 & \ddots & 0 & s & 0 & 0 \\ 0 & 0 & \cdots & 0 & 0 & s & s \end{bmatrix}$$

One difficulty with this simplification is the need for an emigration-adjusted estimate of juvenile survival. When this is unavailable, fecundity rates may still be estimated by starting the population projection at age 2, or, if nearly all birds are pre-breeders by age 7, the population projection may be started at age 8, with $x_1^{(8)} = \psi_B^{(8)} x^{(8)}$, $x_3^{(8,I=0)} = \left(1-\psi_B^{(8)}\right) x^{(8)}$ and all other states set to 0.

The growth rate λ is then estimated by the dominant eigenvalue of $\boldsymbol{\psi}_a$, while the associated eigenvector is used to calculate the stable age-distribution ($w^{(a)}$). Together with $k^{(a)}$, the population size may then be calculated from the number of breeding pairs,

$$N = \frac{2B}{\sum_{a=8}^{n} w^{(a)} k^{(a)}}$$

Uncertainty may be incorporated in these estimates using numerous methods: sampling from the posterior distribution, sampling from normal approximations to the posterior, or using the delta method (Rice 1995). Due to assumptions required about emigration, and the small differences expected between the different methods, the simplest approach is justified.

5.6 Analyses of Gibson's albatrosses

Gibson's albatrosses are biennial breeders, with approximately 5,800 breeding pairs *per annum* (Walker and Elliott 1999). Earlier studies suggested survival rates of approximately 0.97 for males and 0.95 for females, breeding begins at 10-12 years of age, and breeding success ranges between 0.5 and 0.7 (Walker and Elliott 1999, Elliott and Walker 2005, Fletcher et al. 2008). The total population was roughly estimated at 40,000 (Gales 1998). However, given the stable population (Elliott and Walker 2005), the methods described in Chapter 3 suggest that 40,000 individuals would be at the lower end of reasonable estimates, and that 60,000 individuals is a better estimate of the total population size. They breed in the Auckland Islands, primarily on Adams Island where the study area is located (Walker and Elliot 2002). This species is currently listed as *vulnerable* due to limited breeding locations (BirdLife International 2009).

Data was available for 1258 birds observed as breeders (1212 banded as adults and 42 as chicks). Banding of adults began in 1991 and banding of chicks began in 1993 (with increased banding effort from 1995), and data was available through 2006. After banding, birds were recorded as being observed or not in a given year; if observed, their reproductive state was assessed (i.e. breeding, not breeding, etc.). Further, for breeding birds, their reproductive success was also assessed, and gender data was available for most birds banded as adults (see Walker and Elliott 1999 for details). Of the birds banded as chicks, 1094 were included in the analysis, as the remainder were assumed to be too young to return to the colony. Of these, 402 were observed to have returned to the colony, and 42 were observed breeding (Table 5.1). The youngest observed pre-breeder was 3 years old, while the youngest observed breeder was eight.

Due to the high nest-fidelity of the albatrosses studied (Walker and Elliott 1999), birds observed breeding in the study area are unlikely to emigrate, and observed survival of birds banded as adults should represent a value close to true survival, although a few birds at the edge of the study area are known to have moved their nest to outside of the study area (Elliott and Walker 2005). For birds banded as chicks, emigration out of the study area may happen either at the juvenile stage or during the pre-breeder prospecting phase, and survival is confounded with emigration. While the reproductive state of a bird was assessed when re-sighted, the stage of the bird was not. In particular, a bird observed in the study area prior to being observed breeding may be a pre-breeder, a skipping breeder, or a long-term non-breeder. This suggests that a *TPM* similar to Equation 5.13 would be appropriate for this data, with modifications as described below.

Table 5.1. Number of chicks banded (N) for each cohort in the study area, the number observed to have returned to the study area (N_R), the cohort minimum age of first observed return ($\min_R$), the number observed to have bred in the study area (N_B), the cohort minimum age of first observed breeding ($\min_B$), and the number first observed breeding by age.

Cohort		Observed in study area			Observed breeding			Age of first observed breeding						
Year	N	N_R	(%)	$\min_R$	N_B	(%)	$\min_B$	8	9	10	11	12	13	14
1993	2	0	(0)	na	0	(0)	na	0	0	0	0	0	0	0
1994	2	2	(100)	7	1	(50)	13	0	0	0	0	0	1	
1995	38	20	(53)	4	8	(21)	9	0	2	4	1	1		
1996	121	70	(58)	5	23	(19)	8	3	12	7	1			
1997	121	64	(53)	4	7	(6)	8	2	5	0				
1998	144	80	(56)	5	3	(2)	8	3	0					
1999	135	68	(50)	4	0	(0)	na	0						
2000	122	71	(58)	3	0	(0)	na							
2001	58	14	(24)	4	0	(0)	na							
2002	133	13	(10)	3	0	(0)	na							
2003	107	0	(0)	na	0	(0)	na							
2004	111	0	(0)	na	0	(0)	na							

5.6.1 Capture probabilities

Capture probabilities were treated as year-, state-, and gender-specific. It was assumed that juveniles, dead birds, and those that have emigrated could not be observed, so their capture probability was set to 0. Adult birds were first banded in 1991, and the study area was not visited in 1992 (Walker and Elliott 1999), so the first year that adult birds could be observed was 1993. Banding of chicks began in 1993, and the age of first observed return was $\hat{k}_R = 3$. It was therefore assumed that no birds return prior to age 3, so the first year that pre-breeders could be observed was 1995. It was also assumed that prospecting birds and skipping adults (other non-breeders) could have different capture probabilities which incorporate short-term, temporary emigration. In studies where long-term temporary emigration may be a factor, it should be explicitly accounted for in the population model (Jenouvrier et al. 2008). Uniform priors were assigned for the observable states for each gender and year (and breeding status for birds in state (3)), as

$$p^{(s,g,I,y)} \sim \text{Uniform}(0,1)$$

for $s \in \{1,2,3\}$, $g \in \{0,1\}$, $I \in \{0,1 \mid s=3\}$ and $I=1$ otherwise, and *y* from 1993 to 2006 for adults ($I=1$), and *y* from 1996 to 2006 for pre-breeders ($I=0$, $s=3$).

5.6.2 Adult survival and transition parameters

In Fletcher et al. (2008), year-, state-, and gender-specific parameter estimates were calculated for adult survival, transition, and capture probabilities; state and temporal differences in those estimates were of interest. Generally, the amount of year-, state-, and gender-variation was limited (Fletcher et al. 2008). The limited numbers of chicks that had returned to breed, combined with the unobservable nature of the juvenile stage, make it unlikely that temporal variation in recruitment patterns could be adequately explored. This suggests that little insight into recruitment would be gained by including temporal differences in adult transition parameters or survival rates. Further, differences in survival rates amongst adults in different states were relatively small (Fletcher et al. 2008), suggesting that the use of a constant survival rate would not be unreasonable. However, there were substantial differences in capture probabilities over time, state, and gender, so they were not simplified.

All nesting birds in the study area were banded if possible (Walker and Elliott 1999), which means that data was generally collected for both birds in a pair. Because of this, reproductive success data is essentially recorded twice. Similarly, because albatrosses have high mate fidelity, pairs will generally make the same state transitions, so estimates of gender-specific transition parameters will also be correlated. Treating the data as independent and pooling it together would result in overly precise parameter estimates. In order to avoid this problem, gender-specific estimates for breeding success and other adult transition parameters were estimated. Survival for birds in a pair was treated as independent, so adult survival was treated as a constant value for all birds.

These model simplifications are not meant to suggest that state and time effects are not important. Rather, they are designed to simplify the model in areas where simplification is deemed to have little impact on parameters of interest (i.e. age at first return and breeding), and they also reflect the available data. In particular, the assumption that all adults, regardless of gender, year, state or individual quality, have the same underlying survival rate is patently false; however, it is a useful anchor for estimating emigration rates and then adjusting the estimated age at first breeding for emigration.

The prior distribution for adult survival incorporated knowledge about other Procellariiformes (Appendix A), and was assumed to be at least 0.8, so,

$$s \sim \text{Uniform}\left(0.8,1\right)$$

Little was known in advance about gender-specific transition probabilities, and so non-informative priors were used for the probabilities of gender-specific breeding success, that a failed breeder would attempt to breed the following year, that an obligate non-breeder would attempt to breed the following year, and that an adult other non-breeder would attempt to breed the following year, so

$$b^{(g)} \sim \text{Uniform}(0,1)\,,$$

$$v^{(g)} \sim \text{Uniform}(0,1)\,,$$

$$\psi_{2,1}^{(g)} \sim \text{Uniform}(0,1)\text{ , and}$$

$$\psi_{3,1}^{(g,A)} \sim \text{Uniform}(0,1)\,.$$

5.6.3 Juvenile survival and transition probabilities

Gender

For birds banded as chicks, gender was unknown. However, because adult transition probabilities depend on gender, gender needed to be estimated. An even gender distribution for chicks was assumed, and the gender of the *i*th bird was given a prior distribution of

$$g^{(i)} \sim \text{Bernoulli}\left(0.5\right)$$

where $g^{(i)} = 1$ indicates a female bird.

Juvenile and pre-breeder survival and emigration

Juveniles were assumed to have survival rate s_2 from banding to age 2, and that this rate was less than adult survival. After age 2, it was assumed that all birds have the same survival rate (s); this combined survival rate was used as a means of adjusting for emigration when calculating mean age at first breeding. While juveniles may have lower (or different) survival rates than older birds, it is difficult to measure this with any accuracy due to the combination of emigration and the unobservable nature of at-sea juveniles. Given the assumption of constant survival from age 2, apparent survival from banding to age 2 ($l_2^A = s_2\left(1-\varepsilon_J\right)$) may be estimated with reasonable precision. Also, due to the limited study period and the inability to observe at-sea juveniles, apparent survival to age 2 was also fixed across time. Hence, the prior distribution assigned to apparent survival from banding to age 2 (survival less emigration) was,

$$s_2^A \sim \text{Uniform}\left(0, s\right)$$

When juveniles returned to the colony as pre-breeders, it was impossible to distinguish between them and adult other non-breeders without a modelling approach or an ad-hoc decision rule. This distinction is important because, although it was assumed that there are no differences in baseline survival, pre-breeders may still be involved in emigration, which is confounded with estimates of survival. Hence, it is likely that apparent pre-breeder survival would be lower than adult survival.

In general, a modelling approach that treats breeding status (i.e. has the bird ever bred or not) as an unknown but estimable variable allows pre-breeders to be distinguished from adult other non-breeders. Thus, apparent survival ($s_3^{(I)}$) for birds identified as 'other non-breeders' was defined as

$$s_3^{(I)} = \begin{cases} s_P & I = 0 \\ s & I = 1 \end{cases}$$

Again, because skills relevant to survival are likely to have been learned by the age a bird returns to the colony, the difference between adult survival and s_P is likely due to emigration out of the study area, and it was assumed that $s_P = s - \varepsilon_P$. Since $0 \le s_P \le s$, the prior distribution for pre-breeder emigration was,

$$\varepsilon_P \sim \text{Uniform}(0, s)$$

Age at first return

After a period of several years away from the colony, birds may return to the colony as pre-breeders. The minimum age of first return is k_R, and is estimated as the earliest age at which a bird in the data was observed to return. Thus, the age at first return to the colony was a function of age (*a*) and $\hat{k}_R = 3$. Assuming that all birds will eventually return to a colony, the probability that a living bird returns at age *a* ($\psi_R^{(a)}$) is modelled as

$$\begin{aligned} &\text{logit}\left(\psi_R^{(a)}\right) = \beta_0 + \beta_1 (a - 3) && \text{if } a \ge 3 \\ &\psi_R^{(a)} = 0 && \text{if } a < 3 \end{aligned} \tag{5.14}$$

That is, the probability a bird returns to a colony that has not yet returned and is age *a* is modelled as a simple logistic function, provided the bird has reached the minimum age at first return. As in Sec. (5.5), $\beta_0 \sim \text{Normal}(0, \sigma = 10)$, and $\beta_1 \sim \text{Normal}(0, \sigma = 10 \mid \beta_1 > 0)$ priors were assigned, noting that these are non-informative on the logit scale, but with the constraint that $\beta_1 > 0$, forcing all living, non-emigrating birds to eventually return to the colony as pre-breeders.

5.6.4 Models for recruitment to breeding

With limited numbers of birds observed breeding, the recruitment to breeding model potentially will have a large influence on the estimated age at first breeding. Three different parametric models are used to highlight this. Parametric models were chosen because the limited study duration requires projection of recruitment probabilities to age classes beyond those observed. Because of this, the biological plausibility of models for future age classes must be considered. The first model assumes a constant probability of recruitment for all surviving pre-breeders that have not yet bred. This model has the benefit of simplicity, but may be too simple. The second model assumes a logistic function, where the probability that a bird breeds for the first time increases with age to age 10, and then remains constant, so that all birds will become breeders if they live long enough. The third model also assumes a logistic function, but the probability of breeding only increases with age until age 10 and then decreases, so that birds which do not begin breeding by a certain age become long-term non-breeders. Thus, for pre-breeders ($s = 3$, $I = 0$) transitioning to breeding ($s = 1$, $I = 1$), the probability of that transition ($\psi_B^{(a)}$) will be one of three different functions of age.

The effect of the functional form of $\psi_B^{(a)}$ on the estimated age at first breeding will be assessed. In particular, because of the limited study duration, the ability to select an appropriate functional form is limited. The deviance can be used to assess different models for the observed state and capture data, but not for projected age classes. It is therefore important to understand what impact the selected form will have on the estimated age at first breeding.

Model 1: Constant recruitment probability

In this model, it was assumed that the probability that a pre-breeders breeds for the first time is constant beyond minimum age at first reproduction (k_B), estimated as the minimum age a bird banded as a chick was observed to breed in the data, $\hat{k}_B = 8$, so

$$\psi_B^{(a)} = \begin{cases} 0 & \text{if } a < 8 \\ \psi_B^{(8+)} & \text{if } a \geq 8 \end{cases} \tag{5.15}$$

A $\text{Uniform}(0,1)$ prior was used for $\psi_B^{(8+)}$.

Model 2: Recruitment probability increases with age

In this model, it was assumed that pre-breeders have an increasing probability of breeding as they increase in age, eventually reaching an maximum rate, assumed to occur at age 10. Hence, transition rates for younger birds ($\psi_B^{(a)}$) that also depended on age (*a*) and a minimum age at first reproduction ($\hat{k}_B = 8$), were modelled as,

$$\psi_B^{(a)} = \begin{cases} 0 & \text{if } a < 8 \\ \text{logit}^{-1}\left(\theta_0 + \theta_1(a-8)\right) & \text{if } 8 \leq a < 10 \\ \psi_B^{(10+)} = \text{logit}^{-1}\left(\theta_0 + 2\theta_1\right) & \text{if } a \geq 10 \end{cases} \tag{5.16}$$

As with age at first return, non-informative (on the logit scale) priors were assigned, with the restriction that $\theta_1 > 0$, so $\theta_0 \sim \text{Normal}(0, \sigma = 10)$, and $\theta_1 \sim \text{Normal}(0, \sigma = 10 \mid \theta_1 > 0)$.

Model 3: Recruitment probability increases with age for several years, then decreases

An alternative assumption to increasing transition probabilities with age is that $\psi_B^{(a)}$ increases for some number of years, but then begins to decrease as high-quality individuals have already entered the breeding population. In this model, some living birds enter a perpetual 'pre-breeder' or long-term non-breeder state, which can be thought of as an adult which has failed to find a mate, i.e. a bachelor or spinster. With limited data, several assumptions were made for this model. It was assumed that $\psi_B^{(a)}$ increased to age 10, and then decreased in symmetric fashion. The age and the symmetry were chosen to simplify the model; age 10 was chosen for consistency with estimates of mean age at first breeding for other albatross species (Appendix A). As in Model (2), $\psi_B^{(a)}$ was modelled using a logistic function as

$$\psi_B^{(a)} = \begin{cases} 0 & \text{if } a < 8 \\ \text{logit}^{-1}\left(\theta_0 + \theta_1\left(a-8\right)\right) & \text{if } 8 \le a \le 10 \\ \text{logit}^{-1}\left(\theta_0 + 2\theta_1 - \theta_1\left(a-10\right)\right) & \text{if } a > 10 \end{cases} \qquad (5.17)$$

Priors for this model were $\theta_0 \sim \text{Normal}\left(0, \sigma = 10\right)$, and $\theta_1 \sim \text{Normal}\left(0, \sigma = 10 \mid \theta_1 > 0\right)$.

The three models can yield substantially different distributions of α_B and estimates of $E\left(\alpha_B\right)$, and the ability to distinguish between them is limited by the number of birds observed breeding and the study length. The fit of Model (1) versus Models (2 or 3) may be determined by a relatively short study, due to substantial differences in the distribution of α_B for early age classes. Selecting between Models (2 & 3) is more difficult, as they are identical until age 10, and therefore require a longer study. For example, suppose for Model (1) that $\psi_B^{(8+)} = 0.15$, and for Models (2 & 3) that

$\theta_0 = -2.5$, and $\theta_1 = 0.5$; further, suppose that all but a negligible proportion of juveniles have returned by age 7, and that survival is $s = 0.95$. The mean ages at first breeding for Models (1 & 2) would be similar (12.2 versus 12.3), while the mean age at first breeding for Model (3) would be 10.2. However, the distributions of the age at first breeding are quite different (Figure 5.2 (a,c,e)) due to the different functional forms of $\psi_B^{(a)}$ (Figure 5.2 (b, d, f)). In particular, Models (1 & 2) project that >5% of birds will first breed at ages 20+ with these assumed parameters, while Model (3) forces older non-breeders into a perpetual bachelor or spinster state until death. The absence of older first-time breeders then results in a lower mean age at first breeding for Model (3), with approximate agreement between the mean and the mode of the distribution.

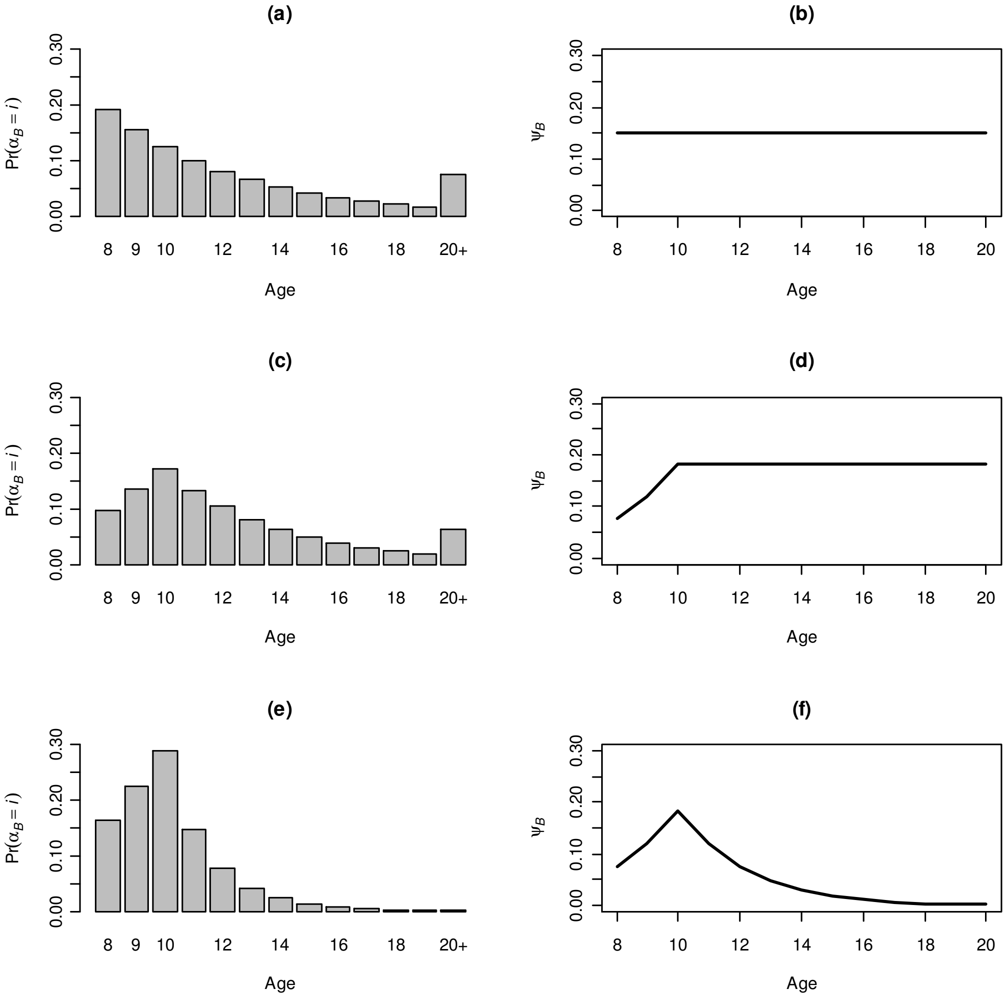

Figure 5.2. $\Pr\left(\alpha_B = i\right)$ from age $i = 8$ for three models of $\psi_B^{(a)}$. Plots (a, b) refer to Model (1) with $\psi_B^{(8+)} = 0.15$. Plots (c, d) refer to Model (2), and plots (e, f) refer to Model (3), with $\theta_0 = -2.5$, and $\theta_1 = 0.5$. Survival was assumed to be $s = 0.95$. $\psi_B^{(a)}$ was drawn as a continuous function for visual ease, but is only evaluated at integer values.

5.6.5 Transition probability matrix for Gibson's albatrosses

The analysis approach in Section 5.5 forms the basis for this analysis, but with some modifications. Gender must be included because of its importance to the adult analysis, and a gender-, age-, and breeding status-specific *TPM* was estimated in an analogous fashion to Equation 5.13, as

$$TPM^{(g,a,I)} = \begin{pmatrix} \left(1-b^{(g)}\right)v^{(g)}\,s & b^{(g)}\,s & \left(1-b^{(g)}\right)\left(1-v^{(g)}\right)s & 0 & 1-s \\ \psi_{2,1}^{(g)}\,s & 0 & \left(1-\psi_{2,1}^{(g)}\right)s & 0 & 1-s \\ \psi_{3,1}^{(g,a+1,I)}\,s_3^{(I)} & 0 & \left(1-\psi_{3,1}^{(g,a+1,I)}\right)s_3^{(I)} & 0 & 1-s_3^{(I)} \\ 0 & 0 & \psi_R^{(a+1)}\,s_J^{(a+1)} & \left(1-\psi_R^{(a+1)}\right)s_J^{(a+1)} & 1-s_J^{(a+1)} \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

(5.18)

where, as in Equation 5.14,

> I is a breeding status indicator variable, equal to 1 for adults, 0 otherwise,
>
> g in a gender indicator variable, equal to 1 for females, 0 for males,
>
> $s_3^{(I=1)} = s$ and $s_3^{(I=0)} = s - \varepsilon_P$,
>
> $s_J^{(2)} = s_2\left(1-\varepsilon_J\right)$ and $s_J^{(a)} = s$ for $a > 2$; and
>
> $\psi_{3,1}^{(g,a,I=0)} = \psi_B^{(a)}$ and, $\forall a, \psi_{3,1}^{(g,a,I=1)} = \psi_{3,1}^{(g,A)}$.

The primary difference between Equation 5.13 and Equation 5.18, aside from the nuisance gender parameter, is that the probability that a bird aged *a* breeds for the first time can be one of three functions of age, and the variability due to the model used can be assessed.

An extension to these models is to allow time-varying parameters, for both adult and juvenile/pre-breeder parameters. Indeed, a cursory examination of the raw data suggests that this may improve model fit. However, the purpose of this analysis is to show the effect of different functional forms for $\psi_B^{(a)}$ on the estimate of mean age at first breeding when the study period is of limited duration. For that reason, the simplicity of time-constant models is preferred.

5.7 Results

5.7.1 Naive estimates

Naive estimates of age at first return and breeding are biased due to emigration and study duration, as exemplified by the simple population model described in Section 5.3. The example presented in Figure 5.1 is based on parameter values that are reasonable for an albatross, albeit for a simplified population model. For this example, the mean age at first breeding (from Equation 5.9) is $E(\alpha_B) = 10.17$ years. If the pre-breeder emigration rate is $\varepsilon_P = 0.05$ and not accounted for, then $E^{(\varepsilon)}(\alpha_B) = 9.57$ years (from Equation 5.11), resulting in a non-negligible bias of -0.6 years. For the same example in a 15-year study, the naive estimate with emigration and data truncation is $E\left(\bar{\alpha}_B^{(N)}\right) = 9.08$ years (from Equations 5.10 & 5.11), more than one year in error. In general, the magnitude of the negative bias increases for shorter studies and for populations with large emigration rates, but a bias of more than one year can easily occur even for relatively long studies with low emigration rates, as in this example.

5.7.2 Simulation study results

A simulation study was described in Section 5.5, where the simulated capture-recapture data was designed to be similar in nature to the Gibson's albatross data or to data that might be collected for other albatrosses. In particular, it incorporated juvenile and pre-breeder emigration, a distinct survival probability to age 2 that is inherently confounded with juvenile emigration, the inability to distinguish pre-breeders from adult non-breeders, and a high capture probability for breeders.

For any individual dataset, variability in parameter estimates will be influenced by study length, the number of birds in the study, capture and transition probabilities, and emigration rates; there may also be bias from the estimation procedure. While use of Bayesian methods introduces some bias through the priors, the simulation was designed to show that, by having an appropriate generating model with well-behaved emigration, it is possible to get reliable estimates of age at first return and age at first breeding even though estimates of $\pi_R^{(i)}$ and $\pi_B^{(i)}$ are known to be biased by emigration.

Age at first return

The mean age at first return for the simulation study was $E\left(\alpha_B\right) = 5.28$ years, while the mean estimate from 25 simulations was 5.29 years, with an estimated bias of $\hat{B}_{\bar{\alpha}_R} = 0.01$ years ($\text{se}\left(\hat{B}_{\bar{\alpha}_R}\right) = 0.05$; 95% CI: -0.11 to 0.12 years). Although age-specific probabilities of returning ($\pi_R^{(i)}$) are biased by the juvenile emigration rate of 20%, the estimated conditional probability of returning given survival ($\psi_R^{(i)}$) has minimal bias; the worst observed age-specific bias in $\psi_R^{(i)}$ was $\hat{B}_{\psi_R^{(6)}} = -0.035$ ($\text{se}\left(\hat{B}_{\psi_R^{(6)}}\right) = 0.016$) at age 6. Bias in the parameters used to estimate $\psi_R^{(i)}$ were also small, with $\hat{B}_{\beta_0} = -0.07$ ($\text{se}\left(\hat{B}_{\beta_0}\right) = 0.07$) and $\hat{B}_{\beta_1} = 0.09$ ($\text{se}\left(\hat{B}_{\beta_1}\right) = 0.06$).

Age at first breeding

The mean age at first breeding for this population model was $E(\alpha_B) = 13.7$ years. The number of simulations ($R = 25$) was designed so that the standard error for the bias of age at first breeding would be approximately 0.1. After 25 simulations, the estimated bias in mean age at first breeding was $\hat{B}_{\bar{\alpha}_B} = -0.04$ years ($\text{se}\left(\hat{B}_{\bar{\alpha}_B}\right) = 0.11$; 95% CI: -0.27 to 0.19 years). As expected, the level of bias in the mean age at first breeding is small when using the correct model, even though its components are known to be biased. The mean estimated probability that a bird aged 8 or older bred for the first time was $\bar{\hat{\psi}}_B^{(8+)} = 0.105$, compared to the actual value of 0.1, giving an estimated bias of $\hat{B}_{\psi_B^{(8+)}} = 0.005$ ($\text{se}\left(\hat{B}_{\psi_B^{(8+)}}\right) = 0.003$).

The mean naive estimate of mean age at first breeding for these 12 year studies (5 years beyond the age at which the first birds began to breed) was 9.6 years, with an estimated bias of $\hat{B}_{\bar{\alpha}_B^{(N)}} = -4.12$ years (95% CI: -4.17 to -4.07 years). Clearly, for this particular population model and a 12-year study, the naive estimate of mean age at first breeding would be unacceptable.

Bias in other parameters

Estimated bias for survival, pre-breeder emigration, and adult transition parameters were all negligible (Table 5.2). Combined with the results from age at first return and age at first breeding, this modelling approach – where transition probabilities are a function of a latent variable that must also be estimated, where emigration plays a confounding role, and where pre-breeders and adult other non-breeders can not be distinguished from each other – is able to successfully estimate the parameters that generated the data.

Table 5.2. Mean parameter estimate ($\bar{\hat{\zeta}}$) from 25 simulations, actual parameter value (ζ), estimated bias ($\hat{B}_\zeta$), and standard error of the estimated bias ($\mathrm{se}\left(\hat{B}_\zeta\right)$).

Parameter	$\bar{\hat{\zeta}}$	ζ	$\hat{B}_\zeta$	$\mathrm{se}\left(\hat{B}_\zeta\right)$
b	0.60	0.60	0.001	0.003
v	0.61	0.60	0.007	0.004
$\psi_{2,1}$	0.80	0.80	0.000	0.003
$\psi_{3,1}^{(A)}$	0.50	0.50	0.003	0.004
s	0.95	0.95	0.001	0.001
$s_J^{(2)}$	0.73	0.72	0.013	0.014
ε_P	0.06	0.05	0.005	0.006
p_1	0.95	0.95	-0.004	0.002
$p_3^{(I=1)}$	0.60	0.60	0.005	0.006
$p_3^{(I=0)}$	0.20	0.20	0.000	0.003

5.7.3 Results for the study of Gibson's albatrosses

The delayed maturity of Gibson's albatrosses and the study length make it difficult to accurately estimate α_B without strong model assumptions. While there were 563 birds that had the potential to reach age 8 by 2006, 284 that could reach age 10, and 164 that could reach age 11, there were only four that had the potential to reach age 13. Thus, the estimated minimum age at first breeding ($\hat{k}_B = 8$) is based on a reasonable sample size, but it is unlikely that the full distribution of age of first breeding has been observed. That is, it is quite likely that many birds will not begin breeding until later ages, but this study was not able to observe them. Instead, three different population models that extrapolated estimates to older age classes were used to estimate the mean age at first breeding; of these three, Model (3) had the smallest deviance (29040 versus 29090 (Model (1)) and 29110 (Model (2))). However, it is unclear how the different models would behave if data were available for the extrapolated age classes. While Model (3) may be the preferred model of these three, because of the extrapolation, all were used to qualitatively assess variability in parameter estimates.

A *TPM* that incorporated well-behaved emigration was assumed for the analysis (Equation 5.18), along with simplifications of adult parameters compared to other analyses of the data (e.g. Walker and Elliott 2005, Fletcher et al. 2008). In particular, an average adult survival estimate was calculated; this value was used as a means of estimating pre-breeder emigration.

Using OpenBUGS (Thomas et al. 2006), three Markov chains were run for 30,000 iterations, with the first 15,000 iterations discarded as burn-in. Monte Carlo error for all parameters was at least one order of magnitude less than the standard deviation of the parameter estimate. Graphical displays of histories for each chain, and of the Gelman-Rubin diagnostic (Brooks and Gelman 1998), suggested good Monte Carlo convergence for all parameters.

Age at first return

The probability a juvenile bird aged *a* that has not yet returned will return (given survival) is estimated by $\operatorname{logit}\left(\hat{\psi}_R^{(a)}\right) = -2.7 + 1.1(a-3)$ for $a \geq 3$ (from Model (3), estimates for β_0 and β_1 from the other models were within ± 0.1 of these). This suggests that nearly 97% of birds return as pre-breeders prior to the age 8 (Figure 5.3), when the first birds begin to breed, with mean age at first return of 5.3 (95% CI: 5.0 – 5.6) years; estimates from the other models were similar (Table 5.3). Combined with survival estimates, this suggests that 63% (95% CI: 58 – 68%) of birds banded as chicks will return to the study area, consistent with observed rates above 50% for the 1995 through 2000 cohorts (Table 5.1).

Table 5.3. Estimated mean age at first return, $E(\alpha_R)$, and first breeding, $E(\alpha_B)$, for Gibson's albatrosses by recruitment to breeding model.

	Estimate (95% CI)		
Parameter	Model (1)	Model (2)	Model (3)
$E(\alpha_R)$	5.3 (5.1 - 5.6)	5.3 (5.1 - 5.6)	5.3 (5.0 - 5.6)
$E(\alpha_B)$	15.0 (13.7 - 16.3)	13.7 (12.4 - 15.2)	10.3 (9.9 - 11.5)

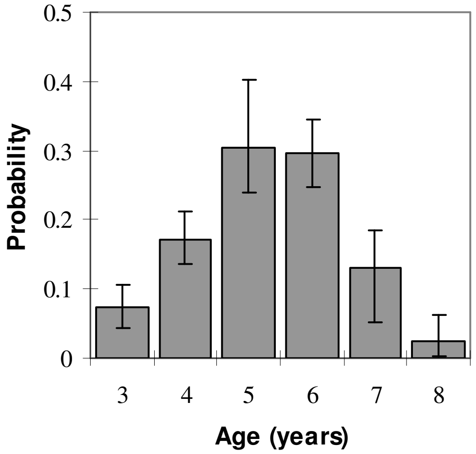

Figure 5.3. The distribution of age at first return (α_R) amongst Gibson's albatrosses. Values presented are based on Model (3); estimates of $\Pr(\alpha_R = a)$ from the other models were similar. Error bars represent the limits of the 95% CI.

Age at first breeding

The estimated mean and distribution of age at first breeding was highly model-dependent (Figures 5.4 – 5.6, Table 5.3). Estimates of $E(\alpha_B)$ ranged from 10.3 years (Model (3)) to 15.0 years (Model (1)). For Model (1), the assumption of constant recruitment rates for birds from the age of 8 onwards creates a distribution of α_B with a mode at age 8, as mortality reduces the size of later age classes. Since the estimated constant was low ($\psi_B^{(8+)} = 0.08$; 95% CI: 0.06 – 0.11), the distribution has a long tail, with >20% of birds predicted to breed from the age of 20 (Figure 5.4), leading to the large estimate of $E(\alpha_B)$. However, the mode at age 8 is inconsistent with the observed age at first breeding. While emigration will cause a discrepancy between the observed and actual age at first breeding for older age classes (even for long-term studies with perfect observation), it will have minimal effect on early age classes. This, combined with the long tail, suggests that Model (1) could be improved upon.

In Model (2), $\psi_B^{(a)}$ increases to age 10 before remaining constant, and the mode of the distribution of α_B changes to a more realistic age 10 (Figure 5.5). However, $\psi_B^{(10+)} = 0.14$ (95% CI: 0.09 – 0.20) is still low, again leading to a long tail, with approximately 12% of birds breeding for the first time from the age of 20. From Model (2), the mean age at first breeding, influenced by the long tail, is estimated as 13.7 (95% CI: 12.4 – 15.2) years.

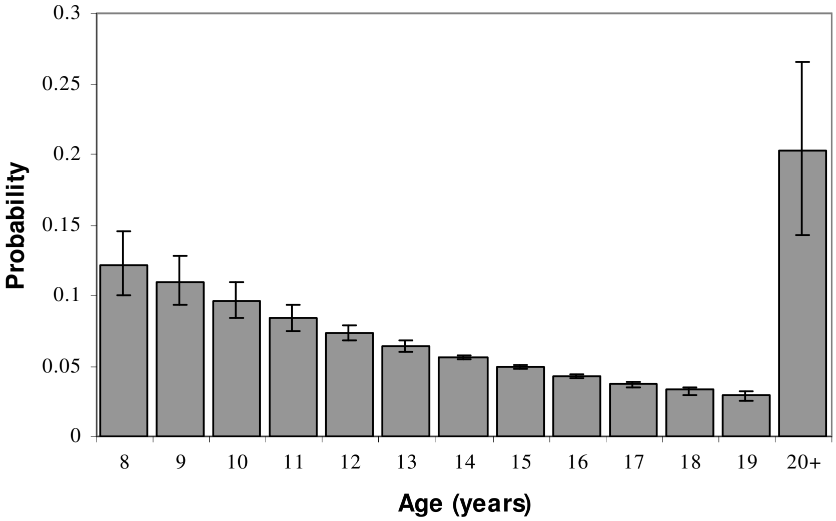

Figure 5.4. Estimated distribution of α_B for Model (1) showing the large proportion of birds predicted not to bred until age 20+. Error bars represent the limits of the 95% CI.

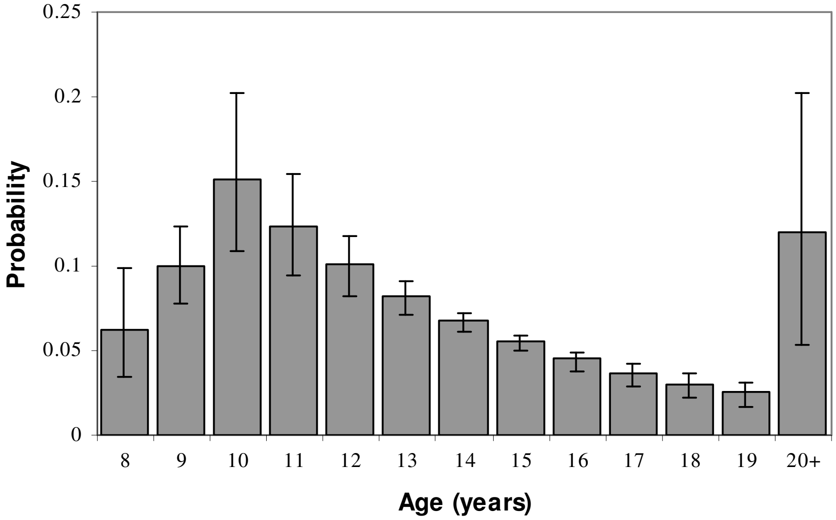

Figure 5.5. Estimated distribution of α_R for Model (2) showing a more realistic shape for early age classes compared to Model (1), but still with a large proportion of birds predicted not to bred until age 20+.

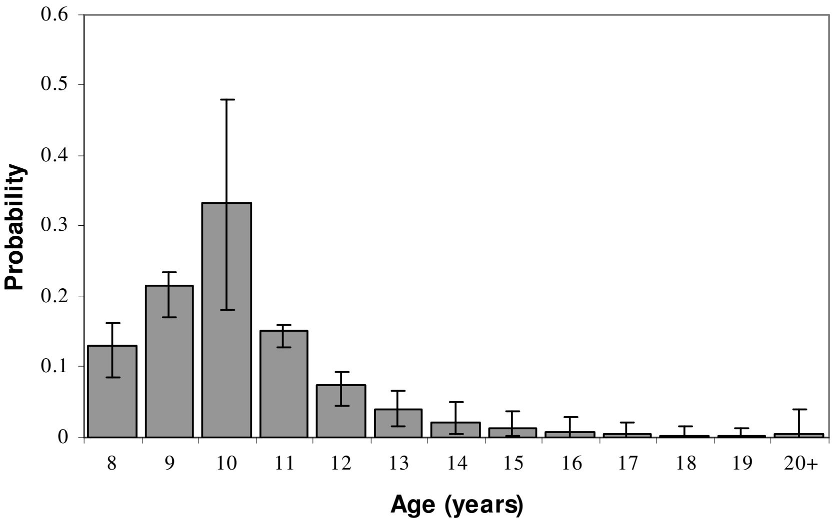

Figure 5.6. Estimated distribution of α_R for Model (3) showing a more realistic shape for early age classes compared to Model (1), and with few birds breeding beyond the age of 16.

Model (3) produces a relatively short-tailed distribution with a reasonable shape for early age classes (Figure 5.6), and fits the observed data better than the other models. However, model fit obviously can not be compared for later age classes. The shorter-tail of the third model is due to the assumption that some birds enter a perpetual non-breeding state until death rather than eventually breeding at an older age. Model (3) then results in the lowest estimated mean age at first breeding, 10.3 (95% CI: 9.9 – 11.5) years.

Other parameter estimates

Parameter estimates for adult survival and transition probabilities were similar those in Walker and Elliott (2005) and Fletcher et al. (2008), although in those analyses, year-specific values were estimated. The different recruitment models had negligible effects on survival, emigration, breeding success, and transition parameters (Table

5.4). Average breeding success was approximately 60%, the probabilities that a bird would attempt to breed the following year (given survival) were 65% for a failed breeder, 75-80% for an obligate non-breeder, and 50% for an other non-breeder (Table 5.4). The low level of variation between estimates for males and females could be expected given the high partner fidelity of Gibson's albatrosses. Annual survival from age 2 was estimated as 0.95. Apparent survival from banding to age 2 (e.g. survival confounded with juvenile emigration) was 0.74, and the annual pre-breeder emigration rate was 0.05.

Capture probabilities for pre-breeders prior to 1997 were based on only 4 marked birds; estimated capture rates from 1997 to 2006 are given in Table 5.5. There was substantial temporal variation in capture rates, with a large increase from 2003 – 2005, which could represent increased capture effort. Alternatively, capture rates could also incorporate lack of model fit due to temporal variation in the recruitment process or through temporary emigration. Capture probabilities for adult birds are provided in Table 5.6, showing high capture rates for breeding birds (often close to 1), low capture rates for obligate non-breeders (the long breeding cycle means that some obligate non-breeders do not leave the colony until the next field season begins), and variable capture rates for other non-breeders.

Population projections

The population growth rate and size may also be estimated from this data. However, the limited number of birds banded as chicks observed breeding, and the resulting uncertainty in the recruitment to breeding process, means that these estimates may have substantial bias from use of an incorrect model. Noting that nearly all birds recruited prior to age 8, fecundity rates were based on the assumption that all living birds were pre-breeders at age 7. Parameter estimates were assumed to follow approximate normality, and sampled $N = 9,999$ times from Model (3), which fit the observed data best. All estimates were assumed to be independent except θ_0 and θ_1, which were negatively correlated with each other ($r = -0.8$), and so were sampled from a multivariate normal distribution. For transitions with gender-specific values, the estimates for females were used.

Age-specific fecundity rates reached 0.06 (95% CI: 0.04 – 0.10) for older age classes (with $\boldsymbol{\psi}_a$ based on 20 age classes, where the last age class included birds aged 20 or greater); around 20% of older age birds were estimated to breed each year. Fecundity rates were reasonably stable from age 10 onwards, while 8 and 9 year old birds had approximately 0.25 and 0.5 the fecundity of birds aged 10 or greater. Assuming that true survival from banding to age 2 was between the lower bound (0.67) and adult survival (i.e. $s_2 \sim U(0.67, s)$, the estimated population growth rate was $\hat{\lambda} = 0.99$ (95% CI: 0.98 – 1.00), consistent with the estimated stable population (Elliott and Walker 2005).

Walker and Elliott (1999) estimated the number of breeding pairs of Gibson's albatrosses at 5,831 pairs *per annum*, based on five years of surveys and a small amount of extrapolation. In 1997, the survey began earlier than in other years and more birds were observed (7,417 pairs); the difference could be due to failed breeders who abandoned their nests (Walker and Elliott 1999). This suggests that there may be some negative bias in the estimate of *B*. Ignoring any temporal trends, and assuming the counts followed a log-normal distribution, the coefficient of variation of *B* was

$CV_{\hat{B}} \approx 0.1$. Sampling from this distribution, and combining the results with the sampled matrix models, provides a population estimate of $\hat{N} = 80,000$ (95% CI: 60,000 – 110,000) birds, with 20th percentile estimate $N_{\min} = 70,000$; values were rounded to the nearest 5,000. Of these, 24,000 (95% CI: 20,000 – 29,000) birds were estimated to have bred at least once; this estimate was similar for all three models.

Projections may also be made from the other two models, although poorer model fit suggests that these estimates should be down weighted. Using Model (1), fecundity reached 0.12, but took nearly 30 years to stabilise; this was due to the skewed distribution of α_B, and the large proportion of breeders that did not begin breeding until later age classes. This model predicts $\hat{\lambda} = 1.01$ (95% CI: 1.00 – 1.02), while the estimated population size was $\hat{N} = 55,000$ (95% CI: 45,000 – 70,000; $N_{\min} = 50,000$) birds. From Model (2), fecundity eventually reached 0.14, but took nearly 25 years to stabilise. The projected growth rate from Model (2) was $\hat{\lambda} = 1.01$ (95% CI: 1.00 – 1.02), while the estimated population size was $\hat{N} = 50,000$ (95% CI: 40,000 – 60,000; $N_{\min} = 45,000$) birds.

The estimated growth rates differed by 0.02 between Model (3) and Models (1 & 2), and the estimated population size differed by 25,000 to 30,000 birds. Confidence intervals that are conditional on the recruitment to breeding model are overly precise when model-to-model variation is considered. Model (3) fit the observed data best, and should therefore be ranked more highly than the other models. However, the limited amount of data and the unobserved age classes suggest that more observations are necessary before selecting a preferred model or calculating model weights.

Table 5.4. Model-specific transition and survival probabilities showing negligible difference in these parameters due to choice of recruitment function.

Parameter		Model (1)		Model (2)		Model (3)	
		Estimate (95% CI)					
b	males	0.615	(0.595, 0.635)	0.614	(0.595, 0.634)	0.615	(0.595, 0.634)
	females	0.603	(0.583, 0.623)	0.603	(0.583, 0.623)	0.603	(0.583, 0.624)
v	males	0.628	(0.594, 0.661)	0.628	(0.595, 0.662)	0.628	(0.594, 0.661)
	females	0.666	(0.632, 0.699)	0.666	(0.632, 0.699)	0.666	(0.632, 0.699)
$\psi_{2,1}$	males	0.750	(0.727, 0.773)	0.751	(0.727, 0.774)	0.750	(0.726, 0.774)
	females	0.800	(0.776, 0.823)	0.800	(0.776, 0.823)	0.800	(0.776, 0.823)
$\psi_{3,1}^{(A)}$	males	0.509	(0.475, 0.544)	0.509	(0.475, 0.544)	0.509	(0.475, 0.543)
	females	0.489	(0.451, 0.528)	0.489	(0.451, 0.528)	0.490	(0.451, 0.529)
s		0.954	(0.950, 0.959)	0.954	(0.950, 0.959)	0.954	(0.950, 0.959)
s_P		0.906	(0.869, 0.942)	0.907	(0.872, 0.939)	0.906	(0.873, 0.938)
ε_P		0.048	(0.012, 0.086)	0.048	(0.015, 0.082)	0.048	(0.016, 0.082)
$s_J^{(2)}$		0.743	(0.678, 0.812)	0.742	(0.679, 0.808)	0.738	(0.674, 0.803)

Table 5.5. Model-specific capture probabilities for pre-breeders from 1997 – 2006. Prior to 1997, only 4 birds could have been observed in the study area, and only 2 birds were observed to return prior to 2000.

Year	Model (1)	Model (2)	Model (3)
	Estimate (95% CI)		
1997	0.30 (0.01, 0.92)	0.24 (0.01, 0.76)	0.43 (0.02, 0.95)
1998	0.15 (0.02, 0.35)	0.10 (0.02, 0.24)	0.42 (0.03, 0.97)
1999	0.05 (0.01, 0.16)	0.05 (0.01, 0.13)	0.05 (0.01, 0.14)
2000	0.06 (0.02, 0.12)	0.06 (0.02, 0.11)	0.06 (0.02, 0.12)
2001	0.08 (0.04, 0.13)	0.08 (0.04, 0.12)	0.08 (0.04, 0.13)
2002	0.18 (0.14, 0.24)	0.18 (0.14, 0.24)	0.19 (0.13, 0.24)
2003	0.80 (0.74, 0.87)	0.81 (0.75, 0.87)	0.81 (0.75, 0.87)
2004	0.81 (0.74, 0.87)	0.81 (0.75, 0.86)	0.81 (0.75, 0.86)
2005	0.68 (0.61, 0.76)	0.68 (0.60, 0.75)	0.68 (0.61, 0.75)
2006	0.16 (0.12, 0.20)	0.16 (0.12, 0.20)	0.16 (0.12, 0.20)

5.8 Discussion

Age at first breeding is one of two key parameters required for using the *PBR* method, and an underestimate of $E(\alpha_B)$ leads to an overestimate of the maximum annual growth rate; in turn, this could lead to an overharvest of the population (Chapter 2). When capture probabilities of breeding birds is high, as with albatrosses, use of the naive estimator $\bar{\alpha}_B^{(N)}$ may be tempting. However, ignoring the study duration and emigration can cause substantial negative bias (>1 year in magnitude) even in a 15-year study with a 5% annual emigration rate (as in the simplified example of Section 5.3). In the simulation studies of Section 5.4, based on a somewhat more realistic population model and a 12-year study, the mean bias from using $\bar{\alpha}_B^{(N)}$ was -4.12 years. Because the magnitude of the bias can be substantial, and the potential impact of negative bias in $E(\alpha_B)$ is overharvest of the species, the naive estimate of age at first breeding should not be used in conjunction with the *PBR* method for management of albatrosses or similar Procellariiformes.

If the only available estimate of age at first breeding is a naive estimate, and it is also used to estimate the population size (see Chapter 3), the underestimate in the population size and the over-estimate of $\lambda_{\max}$ will, to some degree, cancel each other in the *PBR* calculation. Rather than having off-setting bias in two parameters, if estimates of study duration, pre-breeder survival, and adult survival are available, a better approach would be to assume a simple population model as in Section 5.3, and use Equations 5.10 and 5.11 to adjust the estimate. Alternatively, an ad hoc adjustment such as adding 1 year to the naive estimate may be reasonable when no additional information is available.

For situations where capture-recapture data is available, it is possible to get minimally biased estimates even though survival and emigration are inherently confounded, as long as emigration and survival assumptions are not too distant from the true population structure. However, in practical situations where the study duration is limited, un-testable assumptions must be made about the functional form of recruitment to breeding. In these situations, prudence dictates that variability in $E(\alpha_B)$ due to the functional form should be considered as well.

Fundamental assumptions about survival and emigration were made. In particular, it was assumed that the longer time a pre-breeder went without successfully breeding, the more likely it was to emigrate. This means that, of the birds banded as chicks in the study area, birds that breed at a younger age are more likely to be observed than birds that breed at an older age (i.e. birds that begin breeding later are more likely to have emigrated prior to breeding, supported by Frederiksen and Bregnballe 2001). If capture probabilities of breeding birds are near 1, this means that there is an inherent assumption that the distribution of the observed age at first breeding of birds banded as chicks is skewed to the left compared to the actual age at first breeding due to emigration at the pre-breeder stage. Unfortunately, this assumption can not be tested without auxiliary data.

The recruitment process of seabirds may depend on environmental covariates (Crespin et al. 2006). In the study of Gibson's albatrosses, the estimates of age at first return and breeding were based on a small cross-section of the data over a limited period of time. With the limited data, no attempt was made to incorporate temporal variations. Further, in order to keep the focus on recruitment to breeding, only one model for age at first return was considered. In order to fully examine age at first return, alternatives to Equation 5.14 could be considered. For example, a quadratic logistic model for $\psi_R^{(a)}$ would allow for birds not returning to any colony. An obvious future direction for this work – should the data continue to be collected – is to estimate temporal variation in the recruitment process and consider additional models. This could help determine whether recruitment processes were stable over time, or if environmental covariates or other population effects played a substantial role. In this analysis, the only time-varying parameters were capture probabilities, meaning that they are the only parameters that can absorb temporally-related lack of model fit. Additionally, several more years of data could provide an ability to distinguish between different functional forms for the recruitment to breeding process. In addition to improving estimates of α_B, this could lead to more robust estimates of λ and N from matrix model projections.

In summary, the estimated mean age at first breeding can be severely negatively biased if the naive estimator is used and birds are not followed for a sufficient period of time (Figure 5.1). Instead, modelling approaches based on capture-recapture data can alleviate this bias if assumptions about emigration are met. However, even for lengthy studies, relatively few birds banded as chicks may be observed breeding, and the full distribution of age at first breeding is unlikely to be observed. This means that model assumptions – which may be fundamentally un-testable – can have a large effect on the estimated mean age at first breeding.

Table 5.6. Year- and gender-specific capture probabilities (95% CI) for adult breeders, obligate non-breeders, and other non-breeders based on Model (3). Estimates from Models (1 & 2) were within 0.01 of Model (3) estimates.

	Males		
Year	Breeders	Obl. non-breeders	Other non-breeders
1993	0.98 (0.92 - 1.00)	0.50 (0.02 - 0.97)	0.28 (0.14 - 0.44)
1994	0.95 (0.82 - 1.00)	0.01 (0.00 - 0.04)	0.10 (0.02 - 0.23)
1995	0.99 (0.96 - 1.00)	0.15 (0.08 - 0.23)	0.58 (0.42 - 0.74)
1996	0.99 (0.97 - 1.00)	0.19 (0.12 - 0.26)	0.70 (0.53 - 0.84)
1997	0.99 (0.97 - 1.00)	0.07 (0.04 - 0.12)	0.28 (0.16 - 0.40)
1998	0.99 (0.98 - 1.00)	0.01 (0.00 - 0.03)	0.46 (0.29 - 0.65)
1999	0.99 (0.98 - 1.00)	0.08 (0.04 - 0.13)	0.70 (0.57 - 0.80)
2000	0.97 (0.90 - 1.00)	0.12 (0.08 - 0.18)	0.81 (0.73 - 0.88)
2001	0.99 (0.97 - 1.00)	0.08 (0.03 - 0.15)	0.72 (0.64 - 0.80)
2002	0.99 (0.97 - 1.00)	0.12 (0.08 - 0.18)	0.80 (0.70 - 0.89)
2003	0.99 (0.98 - 1.00)	0.15 (0.09 - 0.22)	0.89 (0.80 - 0.96)
2004	0.99 (0.97 - 1.00)	0.23 (0.16 - 0.31)	0.90 (0.82 - 0.95)
2005	0.97 (0.90 - 1.00)	0.18 (0.12 - 0.25)	0.92 (0.86 - 0.97)
2006	0.49 (0.41 - 0.58)	0.10 (0.04 - 0.18)	0.99 (0.97 - 1.00)
	Females		
	Breeders	Obl. non-breeders	Other non-breeders
1993	0.98 (0.92 - 1.00)	0.50 (0.02 - 0.97)	0.15 (0.05 - 0.32)
1994	0.92 (0.77 - 1.00)	0.01 (0.00 - 0.04)	0.04 (0.00 - 0.14)
1995	0.99 (0.96 - 1.00)	0.14 (0.08 - 0.23)	0.37 (0.21 - 0.55)
1996	0.99 (0.97 - 1.00)	0.12 (0.07 - 0.18)	0.60 (0.44 - 0.75)
1997	0.99 (0.96 - 1.00)	0.05 (0.02 - 0.09)	0.31 (0.19 - 0.45)
1998	0.99 (0.98 - 1.00)	0.01 (0.00 - 0.04)	0.33 (0.19 - 0.47)
1999	0.99 (0.97 - 1.00)	0.07 (0.03 - 0.11)	0.56 (0.44 - 0.68)
2000	0.90 (0.80 - 0.99)	0.10 (0.05 - 0.15)	0.65 (0.54 - 0.75)
2001	0.99 (0.97 - 1.00)	0.11 (0.05 - 0.20)	0.46 (0.36 - 0.54)
2002	0.99 (0.96 - 1.00)	0.09 (0.05 - 0.14)	0.62 (0.52 - 0.72)
2003	0.99 (0.98 - 1.00)	0.14 (0.08 - 0.20)	0.55 (0.43 - 0.67)
2004	0.99 (0.98 - 1.00)	0.16 (0.10 - 0.23)	0.59 (0.46 - 0.71)
2005	0.95 (0.85 - 1.00)	0.11 (0.06 - 0.17)	0.61 (0.51 - 0.71)
2006	0.39 (0.33 - 0.47)	0.07 (0.02 - 0.14)	0.76 (0.63 - 0.92)

5.9 References fro Chapter 5

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Chapter 6. Summary and discussion

Albatrosses and petrels are killed at alarming rates, and it is unclear how many mortalities they can sustain. Population modelling tools were developed to help determine the level of sustainable mortalities based on the minimal amount of demographic data available for most species: an estimate of the number of breeding pairs (B), adult survival (s), and age at first breeding (α). In Chapter 2, a method was described to estimate the potential biological removal (*PBR*) for bird populations that requires knowledge of the population size (N), and the maximum growth rate of the population, $\lambda_{\max}$. Niel and Lebreton (2005) showed how $\lambda_{\max}$ could be determined by s and α. Since B, rather than N, is known for most seabirds, a method was developed in Chapter 3 that estimates N from B, s, and α.

The delayed recruitment process of Procellariiformes such as albatrosses and petrels means that fecundity increases with age, contrary to an assumption used in the calculation of $\lambda_{\max}$. In Chapter 4, a modification of the calculation of generation time was developed for populations where fecundity increases with age; this allows an adjustment in the calculation of $\lambda_{\max}$ for birds through its relationship with generation time ($\overline{T}$). Importantly, an ad hoc adjustment works well when fecundity rates are unknown.

Detailed studies of Procellariiformes are usually based on capture-recapture data. High nest-fidelity means that estimates of s for breeding birds are minimally affected by emigration. Estimates of α based on observed ages of first breeding may be biased by emigration, study length, and capture probabilities. In Chapter 5, a model-based approach is described for capture-recapture data that can achieve reliable estimates for the mean age at first breeding and its distribution.

6.1 The *PBR* method

The *PBR* method was developed for marine mammals (Wade 1998) as a means of making management decisions with minimal demographic data; this is exactly the situation for albatrosses and petrels. It calculates the number of allowable human-caused mortalities based on the maximum excess growth ($R_{\max} = \lambda_{\max} - 1$), an estimate of the population size that accounts for uncertainty ($N_{\min}$, suggested to be the 20th percentile estimate), and a recovery factor f, which incorporates management goals and also protects against bias in the estimate of N or $R_{\max}$. The calculation is given by

$$PBR = \frac{1}{2} R_{\max} N_{\min} f$$

Niel and Lebreton (2005) suggested extending this method to birds, and showed how to calculate $\lambda_{\max}$ given s and α, assuming a simple population model. While the *PBR* method can be applied to a variety of species (Milner-Gulland and Akçakaya 2001), it is especially relevant to Procellariiformes and other long-lived birds, as they share a similar life-history to marine mammals, characterised by high adult survival and delayed maturity. It may be used to set bycatch limits when more detailed data is unavailable, and it may also be used to quickly assess whether estimates of human-caused mortalities are likely to be sustainable, possibly be of concern, or likely to be of concern.

Estimated mortality or harvest rates ($\hat{h}$) can be compared to allowable harvest rates (h_a) and maximum harvest rates ($h_{\max}$), where $h_{\max}$ is the *PBR* estimate for a healthy and perfectly measured population. If $\hat{h} < h_a$, and $\hat{h}$ represents the mortality rate from all human-related sources, then the harvest is likely sustainable. If $h_a < \hat{h} < h_{\max}$, harvest rates may be unsustainable, and further investigation is warranted. If $\hat{h} > h_{\max}$, it is likely that harvest rate are unsustainable. Finally, if $\hat{h} < h_a$ represents only one source of human-related mortalities, and the population is known to be in decline, this suggests that there may be other substantial sources of mortality that need to be quantified.

The *PBR* method is a rule-of-thumb that is very useful when there is limited data available. It is not meant as a replacement for more sophisticated analyses or as an excuse to avoid the expensive task of data collection. Rather, its best use may be as a filter, assigning research money and effort where it is most needed. More sophisticated studies of the greater snow goose (*Anser caerulescens atlanticus*, Gauthier and Brault 1998, Gauthier et al. 2001, Gauthier and Lebreton 2004) and the magpie goose (*Anseranas semipalmata*, Brook and Whitehead 2005) yielded similar estimates to the *PBR* method. However, the arbitrariness of the recovery factor *f* and other uncertainties mean that the range between h_a and $h_{\max}$ may be large when using the *PBR* method, while the other methods yielded more precise estimates of allowable harvest. The minimal demographic data available for New Zealand Procellariiformes suggests that, at present, the *PBR* method could be a valuable management tool.

6.2 Calculating the population size of albatrosses and petrels

Estimating the total population size of albatrosses and petrels is difficult because, typically, only birds involved in the breeding process appear at colonies (Baker et al. 2002). Because of this, the stated population size of petrels and albatrosses is often given as the number of breeding pairs, or a proxy such as the number of nests. This leads to imprecise estimates of the total population size, which are based on the number of breeding pairs times a rule-of-thumb multiplier (Gales 1998, Taylor 2000, Brooke 2004a, Brooke 2004b), with limited information available on how the rule-of-thumb multipliers were derived.

The *PBR* method requires more than this: if the suggestions of Wade (1998) are followed, a 20th percentile estimate of the population size is required ($N_{\min}$). In Chapter 3, rather than selecting an example population model and calculating the rule-of-thumb multiplier (as in Brooke 2004b), a larger set of possible population models were considered. By placing constraints on the growth rate λ, it is possible to determine the proportion of the population that must be breeding, given adult (s) and juvenile (s_J) survival, breeding success (b), and age at first breeding (α). With this, all possible rule-of-thumb multipliers may be calculated, and their variability incorporated into estimates of N.

This methodology can be used given knowledge of individual parameters. Alternatively, bounds on survival and other parameters are automatically created by constraints on λ. Survival of younger birds may be difficult to assess, and so two population models were considered. In the first, it was assumed that yearly survival was s_J until age α. In the second, all ages had survival s. These two models represent bounds on the plausible relationship between juvenile and adult survival; reality is probably in between these two models. In both models, it was assumed that a constant proportion of birds began breeding at age α, which is an over-simplification of reality, where some birds begin breeding at a younger age than others. The estimated rule-of-thumb multipliers did not differ much by population model, suggesting that the relationship between juvenile and adult survival is adequately constrained by λ. Further, they were relatively insensitive to α, and use of the mean age at first breeding should suffice. The most important parameter in determining population size is s, along with the bounds placed on λ.

The suggested rule-of-thumb multiplier generally varies depending on λ; this is especially true for albatrosses. In near-optimal conditions, the population size of albatrosses is 8 to 10 times the number of breeding pairs (Table 3.5). In stable conditions, very few breeding birds are necessary if survival is high, and the rule-of-thumb multiplier could be greater than 12. However, a range of 10 to 12 is more realistic for most stable populations (Table 3.4). High survival and stable growth can only be achieved if there is a large proportion of non-breeding adults or very poor breeding success; this could potentially occur in a very high-density setting, but would be unlikely otherwise. Estimates of $N_{\min}$ are less variable, which is of great benefit for *PBR* calculations, as population trajectories for Procellariiformes are often unknown. A good rule-of-thumb for most albatross species is $N_{\min} = 8 \times B$, and variability in the estimate of *B* can easily be incorporated (Tables 3.4 and 3.5).

For petrels, the rule-of-thumb multiplier of 5 suggested by Brook (2004b) is reasonable for species that begin breeding near age 5 with survival near 0.90, but would be closer to 6 for petrels that begin breeding later ($\alpha \approx 8$) and have higher survival ($s \approx 0.94$). For use with *PBR* calculations, $N_{\min} = 4 \times B$ when B is known performs well for most petrels, reducing to $N_{\min} = 3 \times \hat{B}$ when incorporating variability and $CV_{\hat{B}} = 0.5$ (Tables 3.1 – 3.3).

If the Niel and Lebreton estimate of $\lambda_{\max}$ is calculated based on s and α, and $N_{\min}$ is calculated using the methods from Chapter 3, then the *PBR* calculation may be re-written as $PBR = \tau f \hat{B}$ (Equation 3.11), where τ is a coefficient that incorporates the maximum growth rate, and a species-appropriate population multiplier that incorporates uncertainty in the estimate of the number of breeding pairs. For stable populations, the values for τ range from 0.1 for a petrel with $\alpha \approx 8$, $s \approx 0.94$, and $CV_{\hat{B}} = 0.5$, to 0.2 for a typical albatross species ($\alpha \approx 10$, $s \approx 0.95$) with a perfectly measured population (Table 3.6). That is, the maximum number of mortalities that these populations can sustain ($f = 1$) is less than 0.1 to 0.2 times the number of breeding pairs, and could be as low ($f = 0.1$) as 0.01 to 0.02 times the number of breeding pairs for a management approach that aimed to rebuild a depleted population.

6.3 Estimating generation time when juvenile survival is unknown and fecundity varies with age

The mean generation length can be calculated with knowledge of the population growth rate, and age-specific survival and fecundity rates (Leslie 1966, Gaillard et al. 2005, Niel and Lebreton 2005). Unfortunately, survival rates for juveniles and pre-breeders for many species are difficult to estimate (Schwarz and Arnason 2000). By assuming a population model where fecundity and survival are constant from α, the mean generation length simplifies to $\bar{T} = \alpha + s/(\lambda - s)$ (Equation 4.2), Gaillard et al. 2005, Niel and Lebreton 2005), eliminating the need for fecundity and early age-class survival rates. Niel and Lebreton (2005) used this in their calculation of $\lambda_{\max}$ for birds.

Albatrosses, petrels, and many other species are better described by population models where fecundity increases with age. In these situations, if Equation 4.2 is used, setting α to the age that some animals first breed (the naive approach) can result in substantial negative bias (Table 4.2). If this estimate is then used in calculations of $\lambda_{\max}$ and *PBR*, high levels of overharvest could occur (Table 4.3). For the six species studied by Niel and Lebreton (2005) where the constant-fecundity assumption did not hold, ad hoc additions to α were used to avoid bias in $\lambda_{\max}$.

In Chapter 4, a method was developed to modify Equation 4.2 to correctly calculate mean generation length for a population model where some animals begin breeding at age β, fecundity is constant from $\gamma \geq \beta$, and survival is constant from β. While knowledge of fecundity rates for early age classes relative to fecundity at age γ (relative fecundities) is required, knowledge of absolute fecundity rates is not. More importantly, knowledge of survival rates prior to age β is not required.

The modified formula for generation length (Equation 4.9), while lacking the elegance of Equation 4.2, is straightforward to calculate. It can readily be used with numerical methods to calculate $\lambda_{\max}$ (Equation 4.10), and substantially reduces bias in *PBR* calculations compared to the naive approach (Table 4.3). Importantly, if the constant-fecundity model is assumed when the variable-fecundity model is more appropriate, an ad hoc adjustment to α in the Niel and Lebreton estimate (Equation 2.2) performs nearly as well in calculations of $\lambda_{\max}$ as the estimate based on the varying-fecundity model (Equation 4.10), presumably due to inherent variability and the approximations used developing Equation 2.2. Thus, when data on adult survival, population growth rate, and relative fecundities are available, an exact calculation of generation time can be made and used to estimate $\lambda_{\max}$, but when relative fecundities are unknown, an ad hoc adjustment performs well, too.

6.4 Use of capture-recapture data to estimate the age at first breeding

Age at first breeding is an important population parameter, necessary for *PBR* calculations. For albatrosses and petrels, the long and complex recruitment process means that estimates of age at first breeding can be substantially affected by study length and emigration. Because of this, relying on direct observations can lead to substantial bias in the estimated mean and distribution of the age at first breeding. In Chapter 5, population models were combined with Bayesian methods to analyse simulated and actual capture-recapture data.

Focus was placed on estimating the mean age at first breeding ($E(\alpha_B)$, denoted in Chapter 5 with the subscript *B* to distinguish between recruitment to breeding and the age when returning to the colony, α_R). The mean age at first breeding is biologically interesting, and a logical choice to use in ad hoc adjustments. Simulation studies show that estimates based only on observed data (the naive estimate, $\bar{\alpha}_B^{(N)}$) could have bias in excess of -4 years. Since an underestimate of $E(\alpha_B)$ leads to an overestimate of $\lambda_{\max}$ and *PBR*, $\bar{\alpha}_B^{(N)}$ should not be used for these purposes.

An alternative approach is to combine a population model with capture-recapture data. Reliable estimates of $E(\alpha_B)$ and the distribution of α_B can be achieved if necessary assumptions about emigration are met. However, this requires a reasonable model for the recruitment process. Due to the delayed fecundity of albatrosses and petrels, there may be important age classes with little or no data available. In these cases, it is difficult to determine which recruitment model is best, and the chosen recruitment model can have a large influence on estimates of $E(\alpha_B)$.

6.5 Case study: Gibson's albatross

The methods described in Chapters 2 – 5 can be used to estimate the *PBR* and population parameters for Gibson's albatross (*Diomedea gibsoni*); the estimation process changes based on available data. These estimates can be compared to those easily available in the literature. From the methods of Chapter 2, estimates of survival, age at first breeding, the population size, and its coefficient of variation are need to calculate the *PBR*. Using survival and age at first breeding rates typical for albatrosses (Table A.2; $s = 0.96$, $\alpha = 10$), with $\hat{N} = 40,000$ (Gales 1998) and assuming $CV_N = 0.5$, the maximum growth rate is $\lambda_{\max} = 1.05$ (Equation 2.2), and the allowable harvest rate is $h_a = 0.016f$ (Equation 2.8). Setting $f = 0.1$ because the species is listed as vulnerable suggests an initial *PBR* of 60 birds.

The estimate of the population size may be modified using the methods of Chapter 3. Five years of survey data were available (Walker and Elliott 1999), with the estimated mean number of breeding pairs *per annum* equal to 5,831. Assuming the five estimates follow a log-normal distribution, $CV_{\hat{B}} \approx 0.1$. Noting that the population trajectory is thought to be stable (Elliott and Walker 2005) suggests that $\hat{N} = 70,000$ (90% CI: 30,000 – 130,000), and $N_{\min} = 45,000$. Using this estimate increases the *PBR* to 100 birds, a result of both the increased rule-of-thumb multiplier compared to Gales (1998), and the low coefficient of variation of B.

Further refinement is possible by using the methods from Chapters 4 and 5. Capture-recapture data was used to estimate the age at first breeding and relative fecundities. Using Model (3), which fit the observed data best, the mean generation length was $\bar{T} = 30$ years (Equation 4.9) when $\lambda = 1$; this estimate is sensitive to λ. For example, $\bar{T} = 24$ years when $\lambda = 1.02$, and $\bar{T} = 46$ years when $\lambda = 0.98$. Assuming that the current survival rate (0.95) is close to survival in optimal conditions, the maximum growth rate would be $\lambda_{\max} = 1.055$ (Equation 4.10). If the current survival rate is not optimal, and optimal survival is $s = 0.97$, then $\lambda_{\max} = 1.047$.

The estimated population size from Model (3) was $\hat{N} = 80,000$ (90% CI: 60,000 – 110,000). Using $N_{\min} = 70,000$, combined with the optimistic estimate of $\lambda_{\max}$, increases the *PBR* to 190 birds. However, noting that there was not enough data to select an appropriate recruitment model, the variability in $N_{\min}$ between models suggests a slightly more conservative approach, and setting $N_{\min} = 50,000$ seems reasonable. Further, the current survival estimate is unlikely to be optimal given the stable population trajectory; using $\lambda_{\max} = 1.047$ leads to a *PBR* of 120 birds.

In this example, there was a factor of 2 difference across *PBR* estimates. Compared to the somewhat arbitrary nature of selecting f, this difference is probably acceptable, but still not desirable. In this example, the largest difference came from different estimates of population size. For many species, estimates of the total population size available in literature are not remarkably different from the estimates based on the methods in Chapter 3 (Appendix A), and all estimates are approximate. The largest differences were for biennially-breeding albatrosses, including Gibson's albatrosses. For most other species, differences in *PBR* estimates would likely be less.

With Chapter 2 methods, care must be used in selecting an appropriate values for s and α, as underestimates (especially of survival) lead to an overestimate of *PBR*. Using Chapter 3 methods, s and α are used to estimate $\lambda_{\max}$ and N, and the effect of incorrect values on the PBR are not as severe, as errors in $\lambda_{\max}$ and N are in the opposite direction. Hence, while more accuracy is always desirable, *PBR* calculations based on Chapter 3 methods are reasonably robust. Using methods from Chapters 4 and 5 allows improved estimation of generation time, age at first breeding, and population size, and additional improvement in *PBR* calculations.

6.6 Summary

Albatrosses and petrels are threatened by fisheries related-mortalities, as well as by threats from alien species; most species of albatrosses are threatened with extinction (BirdLife International 2009). This is combined with little demographic information for many species, making informed management decisions difficult to make. What is known is that numerous birds are killed each year, and their ability to sustain additional mortalities is limited.

A primary goal of this work was to help determine the number of albatrosses and petrels that could be killed each year without threatening their populations. This question was addressed using population modelling tools; these tools were developed to use available demographic information. In combination with the rule-of-thumb *PBR* calculation, management decisions can be made using only estimates of s, α, $\hat{B}$, and CV_B. Estimates may be refined to reflect increased knowledge of the population structure.

The focus of this research was applied: how to make decisions with minimal information. However, tools of broader interest were also created. For example, a rule-of-thumb multiplier was created to estimate the total population size of albatrosses and petrels from s, α, $\hat{B}$, and CV_B, while Niel and Lebreton's (2005) estimate of $\overline{T}$ for all animals and $\lambda_{\max}$ for birds was adjusted for the varying-fecundity model.

When making management decisions with minimal information, it is important to illuminate and account for uncertainty, and then determine those species where more knowledge is required. The approaches described in this thesis attempt to do that. Ultimately, it is important to recognise that the tools created here are of most use when minimal information is available; decisions based on minimal information should not be treated as endpoints, but as intermediate steps in the process of good decision making.

6.7 References for Chapter 6

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Appendix A. Potential biological removal of New Zealand albatrosses and petrels

The *PBR* for 22 species and sub-species of New Zealand seabirds is presented using methods from this thesis. Estimates are presented for eleven albatrosses and eleven petrels. In some cases these values are compared to estimates of bycatch. It should be noted that the latter necessarily have limitations in terms of data-quality, assumptions used in the analyses, and pertain to certain areas and years/seasons, and do not equate to the total number of human-caused mortalities worldwide from all possible sources. Further, fisheries employing mitigation techniques catch many fewer seabirds than in past years (SC-CAMLR 2006), so current bycatch levels may be lower. The work in this appendix provides *PBR* estimates assuming minimal information; for some species, it would also be possible to do more sophisticated analyses.

A.1 Methods

Various secondary sources were used to obtain estimates of survival (s), age at first breeding (α), and the number of *per annum* breeding pairs (B), both in New Zealand and worldwide (Gales 1998, Taylor 2000, Schreiber and Burger 2001, Brooke 2004, BirdLife International 2009). Brooke (2004) was used when possible: it is thorough and recent, incorporates estimates from Taylor (2000), and is cited by the other recent sources. Methodology between the various primary sources differs, and estimates were not always available for s and α. Because of this, estimates for similar species (i.e. those in the same genus, or those with similar mass) were grouped; for example, all biennially breeding albatrosses were assumed to have $s = 0.96$ and $\alpha = 10$.

The *PBR* was calculated using Equation 3.11 ($PBR_{3.11} = \tau f \hat{B}$). In this case, the *PBR* is calculated using only s, α, $\hat{B}$, and $CV_{\hat{B}}$ (τ incorporates s, α, and $CV_{\hat{B}}$, as well as λ). Population trends for many species are unknown, but are assumed to be close to 1. The IUCN conservation status for each species was obtained from Brooke (2004) and BirdLife International (2009), and f set according to guidelines in Chapter 2.

Many species have not had a census performed for many years, and census methods have varied (Taylor 2000, Brooke 2004). Unless stated otherwise, I will assume that $CV_{\hat{B}} = 0.5$. The choice of 0.5 for the coefficients of variation is based on the expectation that they will be at least 0.1, and at most 1; 0.5 was used simply because it lies between these two bounds. It would be preferable to have a clearer idea as to the amount of uncertainty in each of the estimates of population size. Additionally, given the age of much of the census data, the potential for bias is high. It is not clear in which direction nor how large such a bias might be. This means that the use of $f = 0.5$ suggested by Wade (1998) to allow for bias should not be relaxed for any of these species.

Table A.1 shows the estimated number of breeding pairs (in New Zealand and worldwide), and the conservation status for each of the species. Table A.2 shows the age at first reproduction and adult survival used in the corresponding estimate of $\lambda_{\max}$ and τ; the value chosen for f; the estimates of *PBR* for the New Zealand and worldwide population; and the estimated worldwide population size. The median population estimate ($N_{0.5}$) is presented based on methods from Chapter 3; the median is less sensitive to λ than the mean, which can be substantially larger than the median for smaller values of λ.

Typically, albatross species have the lowest potential for population increase. In addition, all but one of these species are listed as *threatened*, due to limited breeding ranges, risks from longline fishing, and, in some cases, risks from introduced predators. Due to these factors, the allowable removal rate is less than 0.25% of the population for eight of the eleven albatross species or sub-species. The petrels and shearwaters have somewhat greater potential for growth, and fewer (6 of 11 species) are listed as *threatened.* Therefore, they are able to sustain higher rates of removal than the albatross species, although still usually less than 1%.

A.2 *PBR* calculations for biennially breeding albatrosses

Based on available estimates of age at first breeding and adult survival, all biennially breeding albatross species were assumed to have $s = 0.96$ and $\alpha = 10$. From this, $\lambda_{\max} = 1.05$, and the rule-of-thumb population multiplier (for the median) is $N_{0.5} = 10.3\hat{B}$ when $CV_{\hat{B}} = 0.5$, leading to $\tau = 0.15$.

Antipodean albatross (*Diomedea antipodensis*)

Gibson's albatross (*Diomedea gibsoni*)

There is debate as to whether these are distinct species or sub-species of the same species (Burg and Croxall 2004, Brooke 2004), and they also appear as *Diomedea antipodensis antipodensis* and *Diomedea a. gibsoni*. Biennial breeders, there are approximately 5,100 and 5,800 breeding pair, respectively (Tickell 2000, Walker and Elliott 1999). Total population was estimated by Gales (1998) at 33,000 and 40,000, substantially lower than Chapter 3-based estimates of $N_{0.5} = 53,000$ and $N_{0.5} = 60,000$, respectively. They are currently listed as *vulnerable* due to limited breeding locations, and may be reclassified to *endangered* due to a possible declines in adult survival and productivity (BirdLife International 2009). Consequently, the appropriate recovery factor to minimize extinction risk is $f = 0.1$. This results in *PBR* estimates of 80 and 90 birds for Antipodean and Gibson's albatrosses, respectively. They were frequently caught in tuna longline fisheries from 1987 to 2003, and 58 birds were killed during a single trip in 2006 (BirdLife international 2009). Compared to *PBR* estimates, this suggests that fisheries mortalities may still be a concern. Note that a more thorough examination of Gibson's albatrosses was presented in Chapter 6, resulting in *PBR* estimates between 100 and 120 birds.

Southern Royal albatross (*Diomedea epomophora*)

Northern Royal albatross (*Diomedea sanfordi*)

Southern royal albatrosses number approximately 7,800 breeding pairs, while there are 5,200 breeding pairs of northern royal albatrosses, with a total population of perhaps c.50,000 and c.34,000 (Gales 1998), or $N_{0.5} = 80,000$ and $N_{0.5} = 54,000$, respectively. Southern royal albatrosses are listed as *vulnerable* due to a limited breeding range, while northern royal albatrosses are listed as *endangered* because of decreasing habitat quality, a predicted population decline, and small breeding range (BirdLife International 2009), so $f = 0.1$ for both species. This leads to $PBR = 120$ and $PBR = 80$, for southern and northern royal albatrosses, respectively. Japanese longliners in Australian waters in 1989-1995 may have caused nearly four hundred mortalities in some years (Gales et al. 1998), far greater than suggested mortality limits.

Light-mantled sooty albatross (*Phoebetria palpebrata*)

There are 6,800 breeding pairs in New Zealand, and 22,000 worldwide (Tickell 2000, Brooke 2004). Brooke (2004) estimates c.140,000 birds worldwide, compared to $N_{0.5} = 230,000$; Brooke's multiplier of $N \approx 7B$ is more consistent with an annually breeding species than a biennially breeding one. The species is listed as *near threatened* due to a declining population trend, risk from longline fishing and introduced predators (BirdLife International 2009). The species should be able to sustain 310 mortalities from the New Zealand population, and up to 990 worldwide.

A.3 *PBR* calculations for annually breeding albatrosses

Based on available estimates of age at first breeding and adult survival, all annually breeding albatross species were assumed to have $s = 0.95$ and $\alpha = 8$. From this, $\lambda_{\max} = 1.06$, and the rule-of-thumb population multiplier (for the median) is $N_{0.5} = 5.2\hat{B}$ when $CV_{\hat{B}} = 0.5$, leading to $\tau = 0.10$. The large decrease in τ for annual breeders compared to biennial breeders is due to $\hat{B}$ representing *per annum* breeding pairs.

Southern Buller's albatross (*Thalassarche bulleri bulleri*)

Northern Buller's albatross (*Thalassarche bulleri platei*)

There are approximately 12,000 breeding pairs of race *bulleri* and 18,000 breeding pairs of race *platei*, with possibly 145,000 birds in total for both races (Brooke 2004), similar to $N_{0.5} = 154,000$. Due to its limited breeding range, this species is listed as *near threatened*; it is also commonly caught in the tuna longline fishery (BirdLife International 2009). This leads to *PBR* estimates of 360 and 540 birds, respectively.

White-capped albatross (*Thalassarche steadi*)

This is not a well-studied species; there are c. 75,000 breeding pairs representing perhaps 350,000 birds (Gales 1998, Brooke 2004), similar to $N_{0.5} = 390,000$. The species is listed as *near threatened* due to high bycatch rates (BirdLife International 2009), suggesting that $f = 0.3$ is appropriate, leading to a *PBR* of 2,300. Baker et al. (2007) estimated 7,000 bycatch mortalities annually, well above the *PBR* and possibly at a rate greater than $h_{\max}$, suggesting an urgent need for improved mitigation measures and better understanding of the population.

Chatham albatross (*Thalassarche eremita*)

Nearly the entire population of Chatham Albatrosses breed on The Pyramid, Chatham Islands group, New Zealand (Brooke 2004) and are listed as *critically endangered* due to habitat degradation caused by extreme weather events there (BirdLife International 2009). There are 5,300 nest sites, translating into 4,600 breeding pairs (Robertson et al. 2003). Brooke (2004) estimates 19,000 birds in total, similar to $N_{0.5} = 24,000$. Robertson et al. (2003) $s = 0.87$, substantially lower than other species in g. *Thalassarche*; this estimate is assumed to not represent survival in ideal conditions. While this population may be able to support nearly 50 additional mortalities each year, it is unclear if the selection of $f = 0.1$ is appropriate given its *critically endangered* status.

Campbell albatross (*Thalassarche impavida*)

The Campbell albatross has, from a 1992 census, 26,000 breeding pairs, representing approximately 125,000 birds (Gales 1998), similar to $N_{0.5} = 140,000$), and this population may be slowly increasing (Brooke 2004). Breeding in only one location, the species is listed as *vulnerable*; they are commonly caught in longline and trawl fisheries (BirdLife International 2009). These albatrosses should be able to sustain 260 human-caused mortalities annually.

Salvin's albatross (*Thalassarche salvini*)

There are approximately 32,000 breeding pairs based on a 1998 estimate (Brooke 2004). Gales (1998) estimated 350,000–380,000 birds in total, based primarily on a 1978 count of 77,000 breeding pairs. Adjusting for the difference in the number of breeding pairs between the 1978 and 1998 counts suggests c.150,000 birds, comparable to $N_{0.5} = 170,000$. It is unclear whether the large difference in the number of breeding pairs is due to an actual decrease in the number of breeding pairs or to differences in the methods used in the two surveys (Brooke 2004). This discrepancy shows the potential for substantial bias in estimates of population size. While the population appears to not be at risk from introduced predators, limited breeding habitat has lead to a *vulnerable* listing (Brooke 2004, BirdLife International 2009). Birds are killed in trawl and longline fisheries, with approximately 35 known deaths per year from 1996-2005 in New Zealand fisheries, with an unknown total number of mortalities (BirdLife International 2009). They are able to sustain up to 320 additional mortalities each year.

A.4 *PBR* calculations for petrels

Demographic data was missing for many petrel species; estimates used in the analysis considered birds in the same genus or of similar size. This led to three combinations of α and s: $\alpha = 6$ and $s = 0.93$ for *Pterodoma* and *Puffinus* (<1 kg); $\alpha = 7$ and

$s = 0.94$ for *Procellaria* (about 1 kg); and $\alpha = 8$ and $s = 0.95$ for *Macronectes* (4 – 5 kg, similar to annually breeding albatrosses).

Northern giant petrel (*Macronectes halli*)

There are approximately 2,600 breeding pairs in New Zealand and 12,000 worldwide (Brooke 2004). Brooke (2004) notes that a relatively high proportion of the population are non-breeding adults, and estimates 40,000–50,000 birds worldwide, comparable to $N_{0.5} = 60,000$. The population is considered at risk and has suffered high mortality rates from longline fishing, so is listed as *near threatened*; apparent recent population increases may be due to mitigation measures, and the species could be downlisted in the future (BirdLife International 2009). Annual mortalities should be limited to 360 worldwide, approximately 80 of which may come from the New Zealand population. It has been estimated that, in 1998 alone, between 2,000 and 4,000 were killed in illegal fishing for Patagonian toothfish (*Dissostichus eleginoides*) (SC-CCAMLR 1998), well above the global *PBR*, and possibly causing mortality at a rate greater than $h_{\max}$.

White-chinned petrel (*Procellaria aequinoctialis*)

White-chinned petrels are discussed in detail in chapter 2; a summary follows. White-chinned petrels are the most commonly caught seabird species in the Southern Ocean (Weimerskirch et al. 1999). 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-CAMLR 1998); bycatch rates from other fisheries were also high, but have decreased in recent years (BirdLife International 2009). 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), and the species appears to be undergoing a population decline (Berrow et al. 2000). Due to bycatch rates and the suspected population decline, the species is listed as *vulnerable* (BirdLife International 2009).

There are 210,000 breeding pairs of white-chinned petrels in New Zealand, 2.5 million worldwide, with a total worldwide population of c.7,000,000 birds (Brooke 2004) to $N_{0.5} = 12,000,000$. They may be able to sustain a worldwide PBR of 28,000 and 2,300 in New Zealand. Of these, no more than half should be male, and no more than 20% breeding males. This is well below the levels of mortalities estimated for 1997-1998 for just one fishery, suggesting that they may have been unsustainable.

Grey petrel (*Procellaria cinerea*)

There are 50,000 breeding pairs of grey petrels in New Zealand, and perhaps 100,000 worldwide (Brooke 2004). The total population size is near $N_{0.5} = 480,000$, similar to an earlier estimate of 400,000 (Brooke 2004). The species is also at risk from introduced predators, and is listed as *near threatened*, and may be uplisted in the future (BirdLife International 2009). They are frequently caught in longline fisheries, with more than 2,000 killed annually in New Zealand waters from 1980-2000, and adult females are killed disproportionally (BirdLife International 2009). Given $PBR_{NZ} = 1,700$, fisheries-related mortalities in New Zealand waters may have been unsustainable during that period.

Black Petrel (*Procellaria parkinsoni*)

Black petrel, also known as Parkinson's petrel, number 2,600 breeding pairs, all in New Zealand, and have a total population on the order of 10,000 birds (Brooke 2004). The breeding range has been reduced to two islands, where predation, especially by cats, has detrimental effects, and it is listed as *vulnerable* (Brooke 2004, BirdLife International 2009). While introduced predators are likely to be the largest threat for this species, very little bycatch by commercial fisheries could delay the time to recovery should predation levels be brought under control or increase the risk of extinction in the near term. Because of this, annual human-caused mortality should be less than 30 birds annually. While it is known that some birds are killed in longline fisheries, there is no estimate for the amount (Brooke 2004).

Westland petrel (*Procellaria westlandica*)

The 2,000 breeding pairs, all within New Zealand, represent up to c.20,000 birds (Brooke 2004), or as few as $N_{0.5} = 9,600$. The breeding range is only 3.6 km^2 (Brooke 2004), birds are caught in the tuna longline fisheries of Australia and New Zealand, and the population is threatened by introduced predators, leading to a *vulnerable* listing (BirdLife International 2009). If the impact of introduced predators is mitigated, this population should be able to sustain 20 human-caused mortalities from other sources.

Grey-faced petrel (*Pterodroma macroptera gouldi*)

This race of the great-winged petrel (*Pterodroma macroptera*) breeds at many locations throughout the North Island and numbers 200,000–300,000 breeding pairs (Brooke 2004). The population is estimated at $N_{0.5} = 1,100,000$ (or as few as

600,000–900,000 birds, per Brooke 2004). With numerous breeding locations and a large population not known to be in decline, this species is listed as *least concern*, leading to $PBR = 15,000$.

Magenta petrel (*Pterodroma magentae*)

The magenta petrel, or Chatham Island taiko, breeds only on the main Chatham Island and has a tiny population of 15-25 breeding pairs and perhaps 120 individuals, and the population is listed as *critically endangered* (BirdLife International 2009). Due to these factors, a full population viability analysis (*PVA*) is warranted for this species before determining any allowable mortality. For this species, use of the *PBR* value and its inherent simplifications is not warranted, although the value of zero is presented for comparison to any achieved via a *PVA*.

Buller's shearwater (*Puffinus bulleri*)

While Buller’s shearwater is listed as *vulnerable* due to its limited breeding range (BirdLife International 2009), with nearly all birds breeding on Aorangi or Tawhiti Rahi, the main islands of the Poor Knights Islands, New Zealand (Harper 1983). There were c.200,000 breeding pairs (and roughly as many non-breeding birds as breeding ones) at Aorangi in the early 1980s (Harper 1983). The population increased rapidly at Aorangi following the extirpation of pigs in 1936, presumably via re-colonisation from Tawhiti Rahi (Harper 1983), but there is no knowledge of the population trend on Tawhiti Rahi. The high burrow density on Tawhiti Rahi makes census work difficult to perform without damaging burrows (Harper 1983), so the population size is unknown; a 1943 expedition estimated at least 100,000 birds, and likely 500,000 (Wilson 1959). Assuming 700,000 breeding pairs, recognising that estimates may not be accurate due to the limited census data and its age, there may be $N_{0.5} = 3,200,000$ birds in total. This population should be able to sustain 8,400 additional mortalities.

Flesh-footed shearwater (*Puffinus carneipes*)

There are 38,000 breeding pairs in New Zealand and 220,000 pairs worldwide (Brooke 2004). The estimated population size of $N_{0.5} = 990,000$ is considerably greater than the 650,000 birds estimated by Brooke (2004). Due to the large breeding range and population, this species is listed as *least concern* (BirdLife International 2009), with a worldwide $PBR_W = 13,000$. Up to 5,000 to 6,000 may have been killed annually in the tuna fishery (BirdLife International 2009); if this represents birds from either the New Zealand or Australian population (similar in size to the New Zealand population), it would be greater than $PBR_{NZ} = 2,300$, and harvested at a rate greater than $h_{\max}$. Despite the *least concern* listing, high bycatch rates warrant further attention and study.

Sooty shearwater (*Puffinus griseus*)

There are approximately 5 million breeding pairs in New Zealand and 7 million worldwide, with perhaps over 20 million birds worldwide (Brooke 2004), or as many as $N_{0.5} = 32,000,000$. It is thought that the population is declining, possibly due to climate change, and the species is listed as *near threatened* (BirdLife International 2009). Under the assumption of no selection bias in the bycatch, they should be able to sustain 250,000 additional mortalities, of which no more than 180,000 should come from the New Zealand population. However, while driftnet fisheries killed up to

350,000 birds *per annum* in the past, chick harvest ('muttonbirding') in New Zealand is the primary source of mortality currently, with chick harvests of up to 250,000 annually (Brooke 2004, Hunter and Caswell 2005). While this rate is greater than the *PBR* for the New Zealand population, chick mortalities are not as detrimental as adult mortalities, so it is not immediately clear if this level of harvest is sustainable or not. Hunter and Caswell (2005) detail a matrix model approach that analyzes the differential effect of chick versus adult harvest for sooty shearwaters, and are also unable to conclude if current harvest rates are sustainable or not.

Hutton's shearwater (*Puffinus huttoni*)

There are c.110,000 breeding pairs of Hutton's shearwaters (Brooke 2004), where habitat change in the extremely limited breeding range is the reason for their *endangered* listing (BirdLife International 2009). The population size may be as low as 300,000 (Brooke 2004), or up to $N_{0.5} = 480,000$. This species should be able to sustain nearly 1,300 additional mortalities.

Table A.1. The estimated number of breeding pairs, and the IUCN conservation status, for each of 22 New Zealand albatrosses and petrels; the number breeding in New Zealand (B_{NZ}) and worldwide (B_W) are given.

Common name	Scientific name	B_{NZ}	B_W	Conservation status
Albatrosses	Diomedeidae			
Biennial breeders				
Antipodean Albatross	*Diomedea antipodensis*	5,100	5,100	Vulnerable
Gibson's Albatross	*Diomedea gibsoni*	5,800	5,800	Vulnerable
Southern Royal Albatross	*Diomedea epomophora*	7,800	7,800	Vulnerable
Northern Royal Albatross	*Diomedea sanfordi*	5,200	5,200	Endangered
Light-mantled Sooty Albatross	*Phoebetria palpebrata*	6,800	22,000	Near threatened
Annual breeders				
Southern Buller's Albatross	*Thalassarche bulleri bulleri*	12,000	12,000	Near threatened
Northern Buller's Albatross	*Thalassarche bulleri platei*	18,000	18,000	Near threatened
White-capped Albatross	*Thalassarche steadi*	75,000	75,000	Near threatened
Chatham Albatross	*Thalassarche eremita*	4,600	4,600	Crit. Endangered
Campbell Albatross	*Thalassarche impavida*	26,000	26,000	Vulnerable
Salvin's Albatross	*Thalassarche salvini*	32,000	32,000	Vulnerable
Petrels	Procellariidae			
Northern Giant Petrel	*Macronectes halli*	2,600	12,000	Near threatened
White-chinned Petrel	*Procellaria aequinoctialis*	210,000	2,500,000	Vulnerable
Grey Petrel	*Procellaria cinerea*	50,000	100,000	Near threatened
Black (Parkinson's) Petrel	*Procellaria parkinsoni*	2,600	2,600	Vulnerable
Westland Petrel	*Procellaria westlandica*	2,000	2,000	Vulnerable
Grey-faced Petrel	*Pterodroma macroptera gouldi*	250,000	250,000	Least concern
Magenta Petrel	*Pterodroma magentae*	20	20	Crit. Endangered
Buller's Shearwater	*Puffinus bulleri*	700,000	700,000	Vulnerable
Flesh-footed Shearwater	*Puffinus carneipes*	38,000	220,000	Least concern
Sooty Shearwater	*Puffinus griseus*	5,000,000	7,000,000	Near threatened
Hutton's Shearwater	*Puffinus huttoni*	110,000	110,000	Endangered

Table A.2. Potential biological removal of New Zealand albatrosses and petrels. The age at first breeding (α), adult survival (s), maximum annual growth rate ($\lambda_{\max}$), coefficient for use in Equation 3.11 (τ), recovery factor (f), number of additional mortalities that the New Zealand-based (PBR_{NZ}) and worldwide (PBR_{W}) breeding population may sustain, and a median population estimate ($N_{0.5}$) using methods from Chapter 3.

Common name	α	s	$\lambda_{\max}$	τ	f	PBR_{NZ}	PBR_{W}	$N_{0.5}$
Albatrosses								
Biennial breeders								
Antipodean Albatross	10	0.96	1.05	0.15	0.1	80	80	53,000
Gibson's Albatross	10	0.96	1.05	0.15	0.1	90	90	60,000
Southern Royal Albatross	10	0.96	1.05	0.15	0.1	120	120	80,000
Northern Royal Albatross	10	0.96	1.05	0.15	0.1	80	80	54,000
Light-mantled Sooty Albatross	10	0.96	1.05	0.15	0.3	310	990	230,000
Annual breeders								
Southern Buller's Albatross	8	0.95	1.06	0.10	0.3	360	360	60,000
Northern Buller's Albatross	8	0.95	1.06	0.10	0.3	540	540	94,000
White-capped Albatross	8	0.95	1.06	0.10	0.3	2,300	2,300	390,000
Chatham Albatross	8	0.95	1.06	0.10	0.1	50	50	24,000
Campbell Albatross	8	0.95	1.06	0.10	0.1	260	260	140,000
Salvin's Albatross	8	0.95	1.06	0.10	0.1	320	320	170,000
Petrels								
Northern Giant Petrel	8	0.95	1.06	0.10	0.3	80	360	60,000
White-chinned Petrel	7	0.94	1.07	0.11	0.1	2,300	28,000	12,000,000
Grey Petrel	7	0.94	1.07	0.11	0.3	1,700	3,300	480,000
Black (Parkinson's) Petrel	7	0.94	1.07	0.11	0.1	30	30	12,000
Westland Petrel	7	0.94	1.07	0.11	0.1	20	20	9,600
Grey-faced Petrel	6	0.93	1.09	0.12	0.5	15,000	15,000	1,100,000
Magenta Petrel	6	0.93	1.09	0.12	0.1	0	0	90
Buller's Shearwater	6	0.93	1.09	0.12	0.1	8,400	8,400	3,200,000
Flesh-footed Shearwater	6	0.93	1.09	0.12	0.5	2,300	13,000	990,000
Sooty Shearwater	6	0.93	1.09	0.12	0.3	180,000	250,000	32,000,000
Hutton's Shearwater	6	0.93	1.09	0.12	0.1	1,300	1,300	480,000

A.5 References for Appendix A

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Vita

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