

The potential of integrated modelling in conservation biology: a case study of the black-footed albatross (*Phoebastria nigripes*)

Sophie VÉRAN and Jean-Dominique LEBRETON

Key words and phrases: Albatross; conservation biology; Kalman filter; state-space models.

MSC 2000: Primary 62P10; secondary 92D40.

Abstract: Conservation biology aims at assessing the status of a population, based on information which is often incomplete. Integrated population modelling based on state-space models appears to be a powerful and relevant way of combining into a single likelihood several types of information such as capture-recapture data and population surveys. In this paper, the authors describe the principles of integrated population modelling and they evaluate its performance for conservation biology based on a case study, that of the black-footed albatross, a northern Pacific albatross species suspected to be impacted by longline fishing.

**Le potentiel de la modélisation intégrée en biologie de la conservation :
une étude de cas de l'albatros à pieds noirs (*Phoebastria nigripes*)**

Résumé : La biologie de la conservation vise à évaluer l'état d'une population à l'aide d'informations souvent incomplètes. La modélisation intégrée des populations à l'aide de modèles à espaces d'états est une méthode puissante qui permet de combiner de façon adéquate en une seule vraisemblance plusieurs types d'informations telles que des données de capture-recapture et des inventaires de population. Dans cet article, les auteurs décrivent les principes de la modélisation intégrée des populations et ils en évaluent la performance pour la biologie de préservation à l'aide d'une étude de cas portant sur l'albatros à pieds noirs, une espèce d'albatros vivant dans l'Océan Pacifique Nord vraisemblablement affectée par la pêche palangrière commerciale.

1. INTRODUCTION

Conservation biology often aims at assessing the population status and proposing management actions for endangered or harvested species (Soulé 1987; Gauthier & Lebreton 2004). To this purpose, two main approaches have been traditionally used: analyses of successive surveys of population size and structure on the one hand, and population dynamics modelling on the other. These two approaches are based on quite different sources of information.

In the first approach, the pattern of population change is investigated through more or less sophisticated time series methods to determine the rate of change and variability of population size (Miller & Botkin 1974; Clark 2003). This approach requires reliable repeated surveys, which are often unavailable. Furthermore, observation errors are difficult to incorporate in the classical time series models and are unfortunately often ignored, with, for instance, disastrous consequences on the detection of density-dependence in the rate of population change (Dennis et al. 2006).

Demographic models provide a more process-oriented insight into population dynamics (Caswell & John 1992; Beissinger & Westphal 1998). Such models require estimates of demographic parameters, such as survival probabilities and fecundity (Caswell 2001). Estimates of annual survival probabilities in natural animal populations are usually obtained from capture-mark-recapture sampling, in which animals receive unique individual marks. Subsequent observations of these marked animals, either alive or dead, result in data which are analysed using models incorporating annual probabilities of survival (Lebreton, Burnham, Clobert & Anderson 1992) together with probabilities of detection. These models are the counterpart when there

is incomplete detection of individuals of the discrete time survival models used in human health studies (Lebreton, Pradel & Clobert 1993). The quality and relevance of demographic model results can be highly affected by uncertainties in vital rates estimations and by problems of model validation and structure (Beissinger & Westphal 1998).

Hence, each of these two approaches has severe shortcomings when used by itself. Moreover, so-called “integrated population monitoring” often provides both survey information and demographic data. In this case the two types of information have been until recently always combined in an ad hoc fashion, by visually matching model predictions to population size estimates (Nel, Taylor, Ryan & Cooper 2003; Arnold, Brault & Croxall 2006) without resorting to any analytical tool (Besbeas, Freeman & Morgan 2005). This situation is particularly annoying in conservation biology, in which data are often sparse or fragmentary, needs are urgent, and an optimal use of all existing information is thus badly needed.

Recently, integrated population modelling has appeared as a powerful and relevant way of blending several types of information, by offering the possibility of combining into a single likelihood the information brought by surveys and individual demographic data. Integrated population modelling is based on state-space models (Harvey 1989, pp. 10–11), with various methods of treatment and estimation (Besbeas, Freeman, Morgan & Catchpole 2002; Besbeas, Lebreton & Morgan 2003; Buckland, Newman, Thomas & Koesters 2004; Thomas, Buckland, Newman & Harwood 2005). As it is a recent and still developing methodology, Integrated population modelling has been little used apart illustrative examples (see, however, Gauthier, Besbeas, Lebreton & Morgan 2007). The potential of integrated population modelling for conservation biology is strong, as diagnosis and management actions often have to be taken with the information at hand, stakeholders having limited time and budgets. Integrated population modelling is especially relevant because, in this context, the data are generally incomplete: Integrated population modelling can thus be the glue to assemble in a coherent fashion various pieces of information.

The purpose of this paper is to review the basic ideas of integrated population modelling, to discuss its efficiency, to recommend some specific tools and to propose perspectives for improving its expected impact on conservation biology. As an example a case study we use throughout is that of the impact of incidental by-catch by long-line fisheries of black-footed albatross (*Phoebastria nigripes*), a north Pacific ocean albatross (Cousins & Cooper 2000; Lewison & Crowder 2003). In terms of information available, this example is typical of cases studies in conservation and management of vertebrate populations: while a capture-recapture study provided evidence for a relationship between adult survival and fishing activity (Véran et al. 2007), there is no straightforward estimate available for survival in the first part of life, as is often the case for vertebrates (Clobert & Lebreton 1991). In such a situation can population surveys provide enough information for estimating such a parameter? This question is particularly critical for a long-lived species such as albatross, in which the population growth regime is not very sensitive to immature survival. Then, do population surveys bring further information and do they reinforce the conclusions drawn from the capture-recapture analysis of adult survival?

We present first the albatross case study and the available data (Section 2), then state-space models (Section 3), their statistical treatment by Kalman filtering (Section 4), and their application to the albatross case study (Section 5). The discussion (Section 6) covers perspectives for integrated population modelling in conservation biology.

2. THE BLACK-FOOTED ALBATROSS CASE STUDY

Industrial long-line fishing has been suspected since the 1990s to impact upon black-footed albatross populations by inducing a biologically significant amount of mortality (Cousins & Cooper 2000), as proven for albatross species in the southern Hemisphere (Weimerskirch, Brothers & Jouventin 1997). However, in particular because of the wide range of the species at sea and the diversity of fleets concerned, no precise estimate of by-catch mortality has been available to ascertain this suspicion (Cousins & Cooper 2000; Lewison & Crowder 2003) although educated

guesses of the number caught seem to point to deleterious effects on the population (Niel & Lebreton 2005). As other albatross species, the black-footed albatross is a long-lived species with delayed maturity, first breeding taking place at age 5. But for the breeding season, the albatross spend most of their life at sea. Breeding pairs are faithful for life, and forming a new pair after death of the partner may require some time, a biological feature with key consequences on population dynamics.

The only two sources of information are (a) partial surveys of the number of breeders, (b) capture-recapture data.

- (a) The surveys by the US Fish and Wildlife Service concerned breeding numbers in the three main colonies of the Hawaiian Archipelago: French Frigate Shoals, Midway and Laysan Island. They account for about 75% of the world population of black-footed albatross (Cousins & Cooper 2000). Unavoidably, the investigation is restricted to this segment of the population. The extrapolation to the entire world population implicitly assumes that the portion of the population on the sampled islands did not vary over time. A key feature is that only breeders are surveyed, a large number of non breeders being at sea and not amenable to any kind of count. The survey data provide some evidence of a decline. However, the relationship with total population size depends in a complex fashion of the population structure, and, in the absence of an estimation of survey uncertainty, the significance of the decline cannot be assessed in a straightforward fashion.
- (b) In total, 13854 black-footed albatross chicks have been ringed (with a metal ring from the United States Fish and Wildlife Service) since 1980 on Tern Island ($23^{\circ}45'N$, $166^{\circ}15'W$), in the north western Hawaiian Islands. Regular recaptures of breeding birds started in 1992. The resulting data set made available to us consisted of 2046 capture histories of known age breeding birds over $T = 12$ years (1992–2003), covering thus 11 yearly intervals for survival. These data were analysed by Véran et al. (2007), who related the annual adult survival probability to covariates characterising fishing effort in the Pacific using a linear regression built as a constraint into the capture-recapture model (Clobert & Lebreton 1985; Lebreton, Burnham, Clobert & Anderson 1992). In relation with the sparseness of the data, the low number of years of study (11 years), and the large number of largely collinear candidate covariates, strict rules for protecting the quality of regression were applied, by reducing 8 candidate covariates to 3 uncorrelated ones using principal components analysis, and by using a Bonferroni correction to test for the effect of these 3 resulting covariates. The annual adult survival probability was significantly linked to the second principal component, which, among the 8 original variables, was most strongly correlated with the tonnage of swordfish over the north Pacific. Hence, the results indicated, as expected, a decrease in survival with increasing fishing effort. However, the estimated survival for a fishing effort equal to 0 (corresponding to a negative value of the second principal component) was larger than the baseline survival one could expect for such a species (~ 0.95) and even larger than 1, suggesting a nonlinear relationship for low levels of fishing effort, discussed by Véran et al. (2007).

Again, this case study is thus quite typical of conservation biology, in that both survey and demographic information are sparse and lead only to uncertain answers. A state space model will serve as a link between the two pieces of the puzzle.

3. STATE-SPACE MODELS

A state-space model is made of a state and of an observation equation. The state equation describes the state of the system, here a population vector, over a discrete time scale, while the observation equation relates this state to the measurements of the system, here the partial survey. State-space models are generally used in engineering to estimate the state of the system based

on incomplete observations (through the observation equation) and assuming a perfect knowledge of the behaviour of the system, i.e., of the parameters of the state equation (Harvey 1989, pp. 10–11).

We present here and comment on the specific state equation and observation equation for the black-footed albatross study case.

3.1. State equation.

The state equation relates the population vector of the number of females at time t , N_t , to that at time $t + 1$, N_{t+1} . The expected change over one time step $E(N_{t+1} | N_t)$ is given, as in other state space models for animal populations (Gauthier et al. 2007), by a stage-structured matrix model (Caswell 2001, ch. 2, ch. 4), based on the life cycle of the black-footed albatross (see Table 1). The stages are mutually exclusive. They consist of 8 age classes and 2 adult states, breeder (B), and nonbreeders (NB), respectively. The parameters are presented in Table 2; the transitions between states is illustrated in Figure 1.

TABLE 1: The matrix M used in the state-space model for the black-footed albatross *Phoebastria nigripes*. The expected vector $E(N_{t+1} | N_t)$ of population size at time $t + 1$ is obtained as $M \times N_t$. The parameters are described in the text and in Table 2.

Class	1	2	3	4	5	6	7	8	NB	B
1	0	0	0	0	0	0	0	0	0	$0.5 \times s_1 \times f$
2	s_{imm}	0	0	0	0	0	0	0	0	0
3	0	s_{imm}	0	0	0	0	0	0	0	0
4	0	0	s_{imm}	0	0	0	0	0	0	0
5	0	0	0	s_{imm}	0	0	0	0	0	0
6	0	0	0	0	$s_a(1 - r_5)$	0	0	0	0	0
7	0	0	0	0	0	$s_a(1 - r)$	0	0	0	0
8	0	0	0	0	0	0	$s_a(1 - r)$	0	0	0
NB	0	0	0	0	0	0	0	0	$s_a(1 - b)$	$s_a(1 - s_a)(1 - a)$
B	0	0	0	0	$s_a \times r_5$	$s_a \times r$	$s_a \times r$	s_a	$s_a \times b$	$s_a(1 - s_a)a + s_a^2$

Breeders produce young females that enter the population at the next time step in age class 1: The resulting net fecundity $0.5 \times s_1 \times f$, expressed in females of age 1 produced per female, is the product of the fecundity f (in young fledged per female) by the proportion of female at birth, 0.5, and the survival probability over the 6 months from fledging, i.e., the time they leave the nest, to age 1, s_1 . Survival is assumed to be constant from fledging, at 6 months of age, until age 5. We denote the corresponding annual survival probability as s_{imm} . One thus has $s_1 = s_{imm}^{0.5}$ since s_1 covers 6 months. The overall survival from fledging to age 5, s_I , is thus arbitrarily represented as $s_{imm}^{4.5}$. The assumption of constancy of survival between fledging and age 5 inherent in this decomposition has no effect on the growth rate and adult structure of the model, entirely determined by s_1 . Breeders and nonbreeders over age 5 (i.e., in stages 5, 6, 7, 8, B, NB) are assumed to have the same adult survival probability s_a . Individuals “recruit” by progressively moving to state B, between age 5, the age at first breeding at the population level, and age 8, with respective rates r_5 (at age 5), r (at age 6 and 7), and 1 at age 8, implying full recruitment. Each of the corresponding transition probabilities is obtained as recruitment probability \times survival probability (Table 1). Once they become breeders, individuals breed every year if both members of the couple survive, or if they loose their partner but repair immediately $s_a(1 - s_a)a + s_a^2$. The widow individuals unable to repair in the same year move during the next year to the nonbreeder state $s_a(1 - s_a)(1 - a)$. Nonbreeding individuals breed again when they repair $s_a \times b$; otherwise they remain in the nonbreeding state $s_a(1 - b)$. The relationship taken into

account in the transitions just described between the death of the partner and future reproduction is a specific feature of this model (Véran in preparation). It accounts for a peculiar albatross trait of specific interest in the context of the impact of longline by-catch, as the demographic cost of widowing, in terms of time to form a pair and reproduce again, will tend to increase the demographic impact of by-catch beyond the direct effect on survival. When using the model in practice, annual survival probabilities, and in particular, the adult one s_a will vary over time, for example, in relation to fishing effort. The resulting matrix model is thus $E(N_{t+1} | N_t) = M_t N_t$ where M_t is given in Table 1.

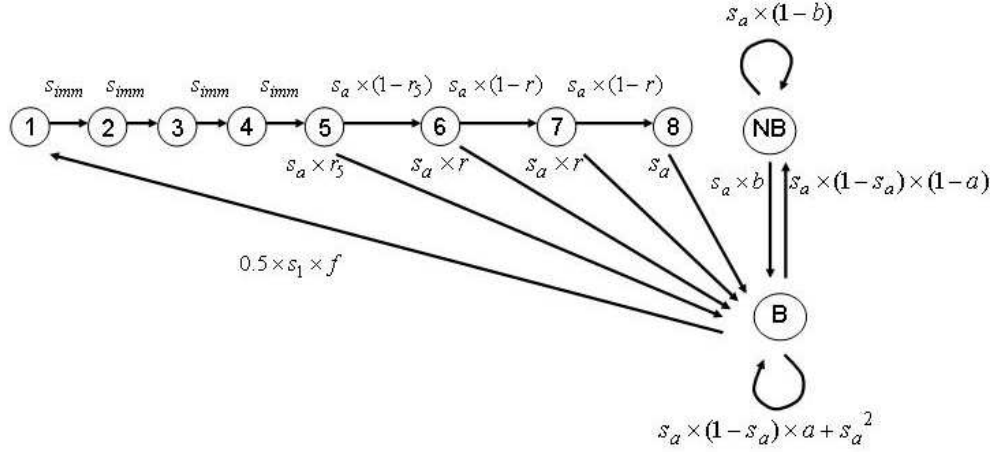


FIGURE 1: Life cycle of the black-footed albatross (*P. nigripes*). From fledging to age 5, the annual survival probability is assumed to be s_{imm} . From 5 years old onwards, the annual survival probability is assumed to be the adult one s_a . A proportion r_5 of 5 year old individuals breeds for the first time. This proportion is r for 6 and 7 year old individuals, and 1 for 8 year old individuals. Once they become breeders, if individuals loose their partner, they form a new pair immediately with probability a . The widows unable to repair the same year become nonbreeders the following year. Nonbreeding individuals have a probability b to pair again and hence to breed again; otherwise they remain in the nonbreeding state. $0.5 \times f$ female chick per female (i.e., pair) fledge at the age of 6 months. They are assumed to have a probability $s_1 = s_{imm}^{0.5}$ to survive over the 6 months that follow, i.e., until one year old.

In the state equation, a random term ε_t accounts for demographic stochasticity, leading to

$$N_{t+1} = \begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \\ N_5 \\ N_6 \\ N_7 \\ N_8 \\ \text{NB} \\ \text{B} \end{pmatrix}_{t+1} = M_t \begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \\ N_5 \\ N_6 \\ N_7 \\ N_8 \\ \text{NB} \\ \text{B} \end{pmatrix}_t + \varepsilon_t. \quad (1)$$

The demographic stochasticity for survival is binomial. An albatross laying only 1 egg, i.e., $f < 1$, that for the fecundity component too. Even with small populations made up of a few hundred individuals, a normal approximation is quite acceptable. Hence the components of ε_t are assumed to be independent and normally distributed with zero means and appropriate binomial variances (see also Besbeas, Freeman, Morgan & Catchpole 2002). For instance the variance for the first component, corresponding to the net fecundity, was $B_t p(1 - p)$ with $p = 0.5 \times f \times s_1$. A key feature is that the state equation is linear. Nonlinearity would correspond biologically to density-dependence; Positive density-dependence, corresponding to a deterioration of demographic performances with increasing population size, will in general not be a priority to consider in conservation biology, dealing with small, often decreasing, largely environment driven populations. Inverse density-dependence at low population size, known as the Allee effect (Courchamp, Clutton-Brock & Grenfell 1999) is on the contrary quite topical in conservation biology for very small populations, although not of concern in our case. It could for instance result from difficulties in finding a partner, as a result of randomly unbalanced sex-ratio. It may require nonlinear state equations and then preclude the formal use of Kalman filtering (see below). An alternative is to think then of population analysis in terms of pseudo-extinction, considering the population viability is definitely impaired below some threshold, corresponding for instance to a deterioration of demographic performance through the Allee effect. Linear state equations seem thus to have a wide applicability in Conservation Biology. For vertebrate population conservation or management concerns, matrix models are commonly built from the knowledge of the life cycle (Caswell 2001, p. 56 ff.), and thus it will be relatively easy to build a linear state equation.

TABLE 2: The demographic parameters of the state space model for the black-footed albatross *Phoebastria nigripes* (Véran & Lebreton, in preparation).

Parameter	Notation	Estimate	Origin
Fecundity	f	0.67	US Fish and Wildlife Service (E. Flint, unpublished data)
Annual Immature survival	s_{imm}	0.771 then estimated in this paper	Based on cohort analysis (Véran & Lebreton, in prep.)
Adult survival	s_a	Estimated in this paper	
Probability of remaining breeder after loss of partner	a	0.34	Based on data of time of repairing (Cousins & Cooper 2000; Véran & Lebreton, in prep.)
Probability of breeding for nonbreeder birds	b	0.62	Based on data of time of repairing (Cousins & Cooper 2000; Véran & Lebreton, in prep.)
Recruitment rate for 5 years old birds	r_5	0.28	Based on cohort analysis (Véran & Lebreton, in prep.)
Recruitment rate for birds > 5 years	r	0.61	Based on cohort analysis (Véran & Lebreton, in prep.)

3.2. Observation equation.

The observation equation links the vector of population size, N_t , with counts of breeding pairs y_t , corresponding to the 10th component of N_t , accounting for survey uncertainty through a random term η_t .

Hence the observation equation is:

$$y_t = AN_t + \eta_t \quad (2)$$

with $A = (0, 0, 0, 0, 0, 0, 0, 0, 0, 1)$.

The random component on population size η_t is assumed to follow a Normal distribution, with mean 0 and variance $\sigma^2 = cB_t^2$. This amounts to assuming a constant coefficient of variation \sqrt{c} for the survey, quite a logical assumption in practice and not a very constraining one given the relatively narrow variation in the number of surveyed breeders over the study years. Moreover, these components are assumed to be independent over time. Gauthier, Besbeas, Lebreton & Morgan (2007) show that replacing the state vector component by the observation, i.e., approximating the variance as cy_t^2 gives quite satisfying results, although it is formally incorrect. At this stage, the only quantities observed are the surveyed numbers of breeders over time $\mathbf{Y}_T = (y_1, \dots, y_T)$, traditionally called the “observations.”

4. KALMAN FILTERING AND OVERALL LIKELIHOOD

4.1. Kalman filter and survey likelihood.

In the simplest case of a linear state-space model, the Kalman filter is a method for recursively forecasting the values of the state vector given the past observations. It is interesting to note that the first mention of a possible application of the Kalman filter in population biology appears in Brillinger (1981), a paper published in *The Canadian Journal of Statistics*. The Kalman filter can be used to build a likelihood of the survey data $L_K(Y, \theta)$, in order to estimate the parameters θ of the matrix model in (1) and the variance parameter in (2). Doing so, one attempts to investigate process (the demographic flows) based on patterns (the surveys) and it is clear that many components of θ will not be separately identifiable. This is why this likelihood will be combined later with other pieces of information on the parameters.

All variables in (1) and (2) being normally distributed, the state vector at time t is also normally distributed, conditional on past observations y_1, \dots, y_{t-1} . In order to fully determine these conditional distributions, it is thus sufficient to obtain their first two moments, which are given directly by the usual form of the Kalman filter as recurrence equations (Harvey 1989, p. 106), and to provide a density function $g(N_0)$ for the distribution of the initial population vector N_0 .

With $\mathbf{Y}_T = (y_1, \dots, y_T)$, the probability density of \mathbf{Y}_T can be expressed as

$$f(\mathbf{Y}_T) = \left\{ \prod_{t=2}^T f(Y_t | \mathbf{Y}_{t-1}, N_0, \theta) \right\} f(Y_1 | N_0, \theta) g(N_0).$$

To initialize the Kalman filter, we ran the time-dependent matrix model over the entire study period, taking the final age-stage distribution and the observed initial number of breeders to produce the expectation of N_0 , following Gauthier, Besbeas, Lebreton & Morgan (2007). The covariance matrix was obtained by assuming a coefficient of variation equal to 10%, independently on all components. A multivariate normal density with this expectation and covariance matrix was used for the probability density of the initial state vector, $g(N_0)$.

A derived technique, Kalman smoothing (Harvey 1989) provides estimates of the state vector, and in turn, the surveyed population size based on all past and future observation $\mathbf{Y}_T = (y_1, \dots, y_T)$. The latter estimates appear as more relevant to an analysis such as ours than the similar one derived from Kalman filtering which only takes into account the information of past surveys.

4.2. Overall likelihood.

The purpose of the integrated population modeling is to estimate parameters by combining different sources of information. Based on the independence of the capture-recapture and the survey data, an overall likelihood can be obtained here as the product of a likelihood for the capture-recapture data and that for the survey data (Besbeas, Freeman, Morgan & Catchpole 2002).

As often, the capture-recapture models and the resulting likelihood considered in this study were unavoidably complex, mostly because of a strong capture heterogeneity that had to be accounted for in the model structure (Véran et al. 2007). The data did not fit a simple Cormack–Jolly–Seber model, and showed strong signs of heterogeneity of capture. Véran et al. (2007) had to use a two-state capture-recapture model which accounted for temporary emigration, with age-dependence in the emigration rate. Survival was considered equal for the two states. This model approximately fitted the data, and was further constrained. As a starting point we use a model with time-dependent annual adult survival probabilities.

To combine the capture-recapture likelihood with the likelihood for the survey data, following (Besbeas, Morgan & Lebreton 2003), we used the approximation of the capture-recapture likelihood based on the asymptotic normal distribution of the estimates. Namely, we used the estimates of the parameters $\hat{\theta}$ of the final capture-recapture model and their estimated covariance matrices $\hat{\Sigma}$ (Véran et al. 2007) to approximate the likelihood of the capture-recapture data by $L_c(X, \theta) \approx \phi(\theta; \hat{\theta}, \hat{\Sigma})$, where $\phi(X; \mu, \Sigma)$ is the probability density of a vector X distributed as $N(\mu, \Sigma)$ (Besbeas, Morgan & Lebreton 2003).

Among the parameters of the state equation, i.e., of the matrix population model, estimates of the parameters a , b , f , and recruitment rates r_i and r_5 were available without information on their uncertainty (Véran & Lebreton, in prep.). Given the high generation time of albatross, these parameters assumed to be known without uncertainty were indeed low sensitivity parameters in the matrix model at the core of the state equation (see Gaillard et al. 2005). As a consequence, assuming a zero variance for these parameters had negligible consequences on the likelihood, as checked by Gauthier, Besbeas, Lebreton & Morgan (2007).

Finally, immature survival, for which no estimate was available, was looked at in two different fashions:

- First, a guess estimate was used, and supposed to be known without uncertainty, to check the behaviour of the overall likelihood by comparison with the capture-recapture analysis, in particular to determine what degree of improvement could be obtained in the models relating adult survival to fishing effort. The value used, $s_I = 0.310$, was deduced from the only available estimate of annual immature survival $s_{imm} = 0.771$ (Cousins & Cooper 2000) using $s_I = s_{imm}^{4.5}$ which also induced $s_1 = s_{imm}^{0.5} = 0.878$.
- Second, in a more tentative fashion, immature survival was considered as part of the parameters to estimate. In this case, the information on immature survival could only come from the survey data.

The overall log-likelihood was obtained as

$$\log L_c(X, \theta) + \log L_k(Y, \theta) \approx \log L_c(X, \theta) + \log \phi(\theta; \hat{\theta}, \hat{\Sigma}).$$

Parameter estimates $\hat{\theta}$ and their variance-covariance were obtained by maximizing the overall likelihood. We used the MATLAB code kindly provided by P. Besbeas for the Kalman filter calculations. A quasi-Newton method (function `fminunc` in MATLAB) was used to minimize with respect to θ the approximated relative deviance $-2\{\log L_c(X, \theta) + \log \phi(\theta; \hat{\theta}, \hat{\Sigma})\}$.

4.3. Model selection.

In a first step, we estimated the annual adult survival probability s_a and the squared coefficient of variation of the observed number of breeders c , by minimizing the approximated relative

deviance of the integrated model above under different constraints; all other parameters were assumed to be known with uncertainty, in particular the guess estimate of immature survival. We considered 3 different models:

- In the first model, denoted $s_a(i)$, the annual adult survival probability was considered as constant over time.
- In the second model, denoted $s_a(t)$, it varied over time.
- In the third model, denoted $s_a(E)$, it was linked to fishing effort E as: $s_a = \beta_0 - \beta_1 E$. The measure of fishing effort was, as explained in the Introduction, the 2nd principal component of 8 fishing effort covariates, selected as the best predictor of adult survival in capture-recapture models by V  ran et al. (2007).

In the latter model the parameters of the regression equation, β_0 and β_1 , replaced the time-dependent annual survival probabilities as parameters in the deviance submitted to minimization. The linear equation above can be derived as an excellent approximation for high baseline survival and relatively low rates of by-catch from standard theory on the dynamics of exploited populations (see, e.g., Lebreton 2005), assuming the number of individuals caught by long lines is proportional to fishing effort.

Model selection was based on the Akaike information criterion (AIC; Lebreton, Burnham, Clobert & Anderson 1992).

The effect of longline fishing was also assessed using a formal test of the null hypothesis $\mathcal{H}_0 : \beta_1 = 0$ versus the alternative hypothesis $\mathcal{H}_1 : \beta_1 \neq 0$, by analysis of deviance (Skalski 1996). This statistic is

$$F = \frac{\text{Dev}(s_a(i)) - \text{Dev}(s_a(E))}{\text{Dev}(s_a(E)) - \text{Dev}(s_a(t))} \times n,$$

in which n is the difference in the number of identifiable parameters between models $s_a(t)$ and $s_a(E)$. It approximately follows under $\mathcal{H}_0 : \beta_1 = 0$ a Fisher–Snedecor distribution with 1 and n degrees of freedom even in presence of unexplained environmental variation (Lebreton & Gimenez, in prep.).

In a second step, we also estimated immature survival, and obtained a profile likelihood 95% confidence interval. As for adult survival, we considered three different models, under the preferred model for adult survival:

- The first one with constant immature survival, denoted as model $s_{imm}(i)$.
- The second with time varying immature survival, denoted as model $s_{imm}(t)$.
- The third one with immature survival function of fishing effort, denoted as model $s_{imm}(E)$. For the sake of parsimony, when used under $s_a(E)$, we used the same slope for young and adults.

5. RESULTS

Among the three model structures for adult survival, model $s_a(E)$ with survival related to fishing effort had the lowest AIC (Table 3). The analysis of deviance was highly significant ($F_{1,9} = 7.03; p = 0.0013$). The estimations of the number of breeders based on the Kalman smoother fit the observations quite satisfactorily (see Figure 2): the smoothed breeding population size was almost always within the 95% confidence interval of the observed breeding population size, except for year 2000 where the smoothed breeding population size was estimated to 46822 individuals for an upper limit of the confidence interval equal to 46109. The estimated coefficient of variation of the surveyed number of breeders was $\sqrt{\hat{c}} = 0.073$. The closeness between the smoothed and the surveyed numbers of breeders (Figure 2) confirmed that

the approximation $\sigma^2 = cy_t^2$ instead of $\sigma^2 = cB_t^2$ was quite reasonable in (2). Among the three models for immature survival, the lowest AIC model was that with constant immature survival (Table 4), although the model with immature survival function of fishing effort ($s_a(E)s_{imm}(E)$) and a same slope for adults and immatures came very close (AIC=202.48 vs. 201.36). Although the sign of the slope was as expected negative, the evidence for an effect of on immature survival was not significant (analysis of deviance, as a one-tailed student's test, $t_9 = 1.33$; $p = 0.1081$).

The estimate of the overall immature survival probability s_I was 0.230 (with a profile likelihood 95% confidence interval equal to [0.155; 0.305], leading for the annual immature survival probability s_{imm} to an estimate equal to 0.721, with a profile likelihood 95% confidence interval equal to [0.661, 0.768].

TABLE 3: Model selection for adult survival probabilities based on the combined likelihood. np is the total number of identifiable parameters, including the coefficient of variation of the census. The preferred model (lowest AIC) is shown in bold.

Model	Deviance	np	QAIC
$s_a(t)$	186.60	12	210.60
$s_a(i)$	202.24	2	206.24
$s_a(E)$	195.38	3	201.38

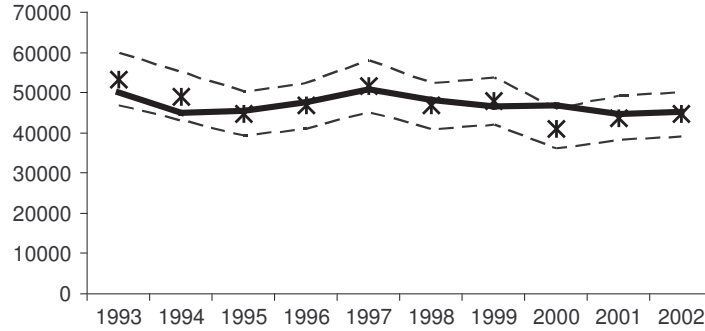


FIGURE 2: Surveyed (*) and smoothed (plain line) with 95% confidence interval (dotted line) number of breeding pairs for the surveyed part of the Hawaii population size of the black-footed albatross. The smoothed values are obtained by the Kalman smoother.

TABLE 4: Model selection for immature survival probability under a model for adult survival assuming a linear relationship with fishing effort. np is the total number of identifiable parameters, including the coefficient of variation of the survey. The preferred model (lowest AIC) is shown in bold. In model $s_a(E)s_{imm}(E)$ (last line), the slope of survival as a function of fishing effort is assumed to be the same for young and adults: this model thus has the same number of parameters as model $s_a(E)s_{imm}(i)$ (line above).

Model	Deviance	np	QAIC
$s_a(E)s_{imm}(t)$	188.80	14	236.80
$s_a(E)s_{imm}(i)$	193.36	4	201.36
$s_a(E)s_{imm}(E)$	194.48	4	202.48

6. DISCUSSION

Our first conclusion is that, in the black-footed albatross example, the integrated population modelling (IPM) was quite efficient in providing an estimate of immature survival, a missing link in the comprehensive view of population dynamics provided by the matrix population model at the core of the state equation. This conclusion is extremely useful and relatively unexpected: the elasticity (Caswell 2001), or relative sensitivity, of the asymptotic growth rate one would deduce from a constant parameter matrix model to changes in immature survival is indeed the inverse of generation time (Lebreton & Clobert 1991; Gaillard et al. 2005). For the black-footed Albatross, with a generation time close to 25 years (Niel & Lebreton 2005), this sensitivity is around 0.04, i.e., a 25% change in immature survival is needed to generate a 1% change in the population growth rate. Obviously this context results in a fairly wide confidence interval for immature survival, carefully estimated here by profile likelihood. However, even when direct capture-recapture approaches such as those based on dead recoveries can be used to estimate immature survival, the precision will often be low. Hence, it is clear that in many cases, IPM will be able to help in estimating parameters difficult to estimate by regular demographic approaches.

TABLE 5: Comparison of parameter estimates and their precision: capture-recapture analysis only versus integrated population modelling (IPM) without estimation of immature survival, and the integrated population modelling with estimation of immature survival. In all cases, adult survival is linearly linked to fishing effort E , as $s_a(i) = \beta_0 + \beta_1 E(i)$ for interval i , a model denoted $s_a(E)$. Since fishing effort is expressed as a standardized covariate, the intercept corresponds to the average fishing effort.

Model	Parameter estimate	
	Intercept β_0 (s.e.)	Slope β_1 (s.e.)
Capture-recapture	0.930 (0.0043)	-0.036 (0.0047)
IPM, $s_a(E)$, without estimation of immature survival	0.926 (0.0029)	-0.034 (0.0044)
IPM, $s_a(E)s_{imm}(i)$, with estimation of immature survival	0.930 (0.0028)	-0.033 (0.0044)

Our second conclusion is that IPM confirmed the capture-recapture based evidence for a relationship between adult survival and fishing effort. The survival estimates were comparable to those obtained by capture-recapture and their precision was slightly increased. One could have expected that the estimation of immature survival would have used all the information available in the population survey. In fact, immature survival was largely determined by the overall population growth rate. In that sense IPM formalizes the ad hoc practice of model tuning, according to which a parameter can be estimated by matching the growth rate of a matrix model to the growth rate estimated from the surveys. However, the surveys have ups and downs which provide information distinct from that in the growth rate and which can translate in the estimates in two different fashions:

1. If these ups and downs do not match changes in adult survival, the most sensitive parameters, they will contribute to increase the estimate of the variance parameter of the observation equation. This will also be the case if the variation in survival estimates is spurious.
2. If they do match changes in survival, they will increase the precision of survival estimates, and lead to a low estimate of the variance parameter in the state equation.

We are clearly in the second case here, as confirmed by the good match between the observed survey of the number of breeders and the smoothed estimates, and the low estimated coefficient of

variation of the survey. This good match also dismisses another possible mechanism, a variation in the number of breeding adults being only the result of a variation in the number of individuals skipping reproduction.

IPM appears thus as efficient and promising for consolidating relationships expressing a variation in demographic parameters explained by environmental covariates. A key perspective for integrated modelling concerns variation over time in parameters unexplained by environmental covariates. When such a time variation will be confirmed by IPM, i.e., when concomitant evidence for such a variation comes from the survey, a capture-recapture model with a random effect will be relevant. Based on the alternative described above, IPM would then appear as natural way to separate a process variance (e.g., in survival) from a sampling variance both in the capture-recapture sampling and in the surveys.

More generally, in conservation biology as well as in other population dynamics studies, IPM will be useful every time there are problems with parameter identifiability. In particular multi-event models (Pradel 2005) which generalise multistate capture-recapture models to uncertain state attribution, appear to be very promising by widely broadening the type of biological information that can be recovered from individual capture-recapture data. The price to pay in terms of parameters identifiability could be to a great extent alleviated by combining these models with survey information by IPM.

Finally, this study confirms that integrated modelling is a very promising method in demography and particularly in conservation biology, a field characterized by often sparse and incomplete data. We expect improved population estimates resulting from IPM to help make population viability analysis, in particular extinction risk analyses, more precise and robust.

ACKNOWLEDGEMENTS

This project was funded by Cooperative Agreement NA17RJ1230 between the Joint Institute for Marine and Atmospheric Research (JIMAR) and the National Oceanic and Atmospheric Administration (NOAA). The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA of any of its subdivisions. The U.S. National Marine Fisheries Service and the U.S. Fish and Wildlife Service provided data. The field research was done on a National Wildlife Refuge by refuge staff and volunteers. We would like to thank the field workers for their hard work banding and reading bands. We thank also P. Besbeas for making available the MATLAB code for the Kalman filter. We also thank an anonymous referee for helpful comments that greatly helped to improve this paper.

REFERENCES

- J. M. Arnold, S. Brault & J. P. Croxall (2006). Albatross populations in peril: a population trajectory for Black-Browed Albatrosses at South Georgia. *Ecological Applications*, 16, 419–432.
- S. R. Beissinger & M. I. Westphal (1998). On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management*, 62, 821–841.
- P. Besbeas, S. A. Freeman & B. J. T. Morgan (2005). The potential of integrated population modelling. *Australian and New Zealand Journal of Statistics*, 47, 35–38.
- P. Besbeas, S. A. Freeman, B. J. T. Morgan & E. A. Catchpole (2002). Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics*, 58, 540–547.
- P. Besbeas, J.-D. Lebreton & B. J. T. Morgan (2003). The efficient integration of abundance and demographic data. *Journal of the Royal Statistical Society Series C: Applied Statistics*, 52, 95–102.
- D. R. Brillinger (1981). Some aspects of modern population mathematics. *The Canadian Journal of Statistics*, 9, 173–194.
- S. T. Buckland, K. B. Newman, L. Thomas & N. B. Koesters (2004). State-space models for the dynamics of wild animal populations. *Ecological Modelling*, 171, 157–175.

- H. Caswell (2001). *Matrix Population Models: Construction, Analysis, and Interpretation*, Second Edition, Sinauer, Sunderland, MA.
- H. Caswell & A. M. John (1992). From individual to the population in demographic models. *Individual-Based Models and Approaches in Ecology* (D. L. DeAngelis, ed.), London, Chapman & Hall, pp. 38–51.
- J. S. Clark (2003). Uncertainty and variability in demography and population growth: A hierarchical approach. *Ecology*, 84, 1370–1381.
- J. Clobert & J.-D. Lebreton (1985). Dépendance de facteurs de milieu dans les estimations de taux de survie par capture-recapture. *Biometrics*, 41, 1031–1037.
- J. Clobert & J.-D. Lebreton (1991). Estimation of demographic parameters in bird populations. *Bird Population Studies: Relevance to Conservation and Management* (C. M. Perrins, J.-D. Lebreton & G. J. M. Hirons, eds.), Oxford University Press, Oxford, pp. 75–104.
- F. Courchamp, T. Clutton-Brock & B. Grenfell (1999). Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution*, 14, 405–410.
- K. L. Cousins & J. Cooper (2000). The population biology of the black-footed albatross in relation to mortality caused by fishing. Technical report for the Western Pacific Regional Fishery Management Council, Honolulu, Hawaii.
- B. Dennis, J. M. Ponciano, S. R. Lele, M. L. Taper & D. F. Staples (2006). Estimating density dependence, process noise, and observation error. *Ecological Monographs*, 76, 323–341.
- J.-M. Gaillard, N. G. Yoccoz, J.-D. Lebreton, C. Bonenfant, S. Devillard, A. Loison, D. Pontier & D. Allaine (2005). Generation time: A reliable metric to measure life-history variation among mammalian populations. *American Naturalist*, 166, 119–123.
- G. Gauthier, P. Besbeas, J.-D. Lebreton & B. J. T. Morgan (2007). Population growth in snow geese: A modeling approach integrating demographic and survey information. *Ecology*, 88, 1420–1429.
- G. Gauthier & J.-D. Lebreton (2004). Population models for Greater Snow Geese: a comparison of different approaches to assess potential impacts of harvest. *Animal Biodiversity and Conservation*, 27, 503–514.
- A. C. Harvey (1989). *Forecasting, Structural Time Series Models and the Kalman Filter*, Cambridge University Press.
- J.-D. Lebreton (2005). Dynamical and statistical models for exploited populations. *Australian and New Zealand Journal of Statistics*, 47, 49–63.
- J.-D. Lebreton, K. P. Burnham, J. Clobert & D. R. Anderson (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, 62, 67–118.
- J.-D. Lebreton & J. Clobert (1991). Bird population dynamics, management, and conservation: the role of mathematical modelling. *Bird Population Studies: Relevance to Conservation and Management* (C. M. Perrins, J.-D. Lebreton & G. J. M. Hirons, eds.), Oxford University Press, pp. 105–125.
- J.-D. Lebreton, R. Pradel & J. Clobert (1993). The statistical analysis of survival in animal populations. *Trends of Research in Ecology and Evolution*, 8, 91–95.
- R. L. Lewison & L. B. Crowder (2003). Estimating fishery bycatch and effects on a vulnerable seabird population. *Ecological Applications*, 13, 743–753.
- R. S. Miller & D. B. Botkin (1974). Endangered Species - models and predictions. *American Scientist*, 62, 172–181.
- D. C. Nel, F. Taylor, P. Ryan & J. Cooper (2003). Population dynamics of the wandering albatross *Diomedea exulans* at Marion Island: longline fishing and environmental influences. *African Journal of Marine Science*, 25, 503–517.
- C. Niel & J.-D. Lebreton (2005). Using demographic invariant to detect overharvested bird populations from incomplete data. *Conservation Biology*, 19, 826–835.

- R. Pradel (2005). Multievent: an extension of multistate capture-recapture models to uncertain states. *Biometrics*, 61, 442–447.
- J. R. Skalski (1996). Regression of abundance estimates from mark-recapture surveys against environmental covariates. *Canadian Journal of Aquatic Sciences*, 53, 196–204.
- M. E. Soulé (1987). *Viable Population for Conservation*. Cambridge University Press.
- L. Thomas, S. T. Buckland, K. B. Newman & J. Harwood (2005). A unified framework for modelling wildlife population dynamics. *Australian and New Zealand Journal of Statistics*, 47, 19–34.
- S. Véran, O. Gimenez, E. Flint, W. Kendall, P. Doherty & J.-D. Lebreton (2007). Quantifying the impact of longline fisheries on adult survival in the black-footed albatross. *Journal of Applied Ecology*, 44, 942–952.
- H. Weimerskirch, N. Brothers & P. Jouventin (1997). Population dynamics of wandering albatross *Diomedea exulans* and amsterdam albatross *D. amsterdamensis* in the indian ocean and their relationship with long-line fisheries: conservation implications. *Biological Conservation*, 79, 257–270.

Received 28 January 2007

Accepted 24 October 2007

Sophie VÉLAN: sveran@nature.berkeley.edu

Department of Environmental Science, Policy and Management
137 Mulford Hall #3114, University of California
Berkeley, CA 94720-3114, USA

Jean-Dominique LEBRETON: jean-dominique.lebreton@cefe.cnrs.fr

Centre d'écologie fonctionnelle et évolutive, UMR 5175
Centre National de la Recherche Scientifique
1919, route de Mende, FR-34293 Montpellier cedex 5, France