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Christine Hunter and Hal Caswell

**Report of the Woods Hole Working Group on Albatross
Demography**

Report
Woods Hole Working Group on Albatross Demography
21–26 September 2004

Rapporteurs:
Christine Hunter
Hal Caswell

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Contents

1	Introduction	3
2	Overview of Demographic Analysis	3
2.1	What do you get <i>out</i> of a demographic model?	3
2.2	What goes <i>into</i> a demographic model	6
2.3	From one population to multipopulation comparisons	7
3	The Life Cycle	7
3.1	The adult life cycle	7
	Many alternatives to Figure 2 are possible:	8
3.2	The juvenile life cycle	8
	Many simplifications of Figure 3(a) are possible:	9
3.3	The entire life cycle	9
	Historical note.	9
4	Data preparation	10
4.1	Data coding	10
	BAS wandering albatross data set	10
	Buller’s data set	11
	Questions and issues related to data coding	11
5	Estimation Procedures	12
5.1	Constraints and parameter estimability	12
5.2	Estimation platforms	12
5.3	Model selection	12
5.4	Goodness-of-fit	13
6	A Wandering Albatross Example	13

7	Next Steps	16
8	Goals For the Next Meeting	17
	Appendices	19
	Appendix A: Participants	19
	Appendix B: Questions of Interest	20
	Appendix C: Buller’s Data Sheet	23
	Formatting Data for Multi-stage Mark-Recapture Analyses	24
	Appendix D: British Antarctic Survey Wandering Albatross Data Sheet	25

The purpose of this report is to document the activities of the first meeting held at Woods Hole Oceanographic Institution, September 21-26, 2004. Based on our fragmentary notes, this report outlines the group’s initial discussions of demographic analyses; including what you get out of a model, what goes into a model and comparative analyses among populations. It outlines the approach we took to developing the life cycle, including the breeding and juvenile portions of the life cycle. It summarizes discussion of data preparation procedures and issues that arose in coding the data. It reports the results of some attempts at parameter estimation and related issues including goodness-of-fit tests, model selection and using additional sources of data. We present one of the preliminary analyses conducted during the workshop as an example. Lastly, the report describes the next steps (i.e. goals for between now and the next meeting) and goals for the next meeting.

1 Introduction

The goal of this working group is to create the best possible demographic analyses of albatross populations. The analyses will include model development, parameter estimation, and model analysis. The hope is that by using a common approach, we will be able to make comparisons across populations and species. We also hope to apply the results in conservation and management. We believe that the potential benefits — to both science and management — of such analyses are enormous. Without this Working Group, it would happen eventually, slowly and in piecemeal fashion, but we are convinced that progress can be made much faster by a cooperative approach. Moreover, the benefits of any such study will be substantially increased by taking a comparative approach across species and locations.

2 Overview of Demographic Analysis

The workshop began with an overview of the capabilities of demographic analysis, a topic that we returned to again at the end of the meeting. Without paying any attention to the enormous effort required to actually construct it, a general demographic model can be written as

$$\mathbf{n}(t + 1) = \mathbf{A}[t, E(t), \mathbf{n}(t)]\mathbf{n}(t) \tag{1}$$

where \mathbf{n} is a population vector (abundances of a chosen set of stages) and $\mathbf{A}[t, E(t), \mathbf{n}(t)]$ is a population projection matrix. A typical element of this matrix, $a_{ij}[t, E(t), \mathbf{n}(t)]$ gives the number of individuals of stage i at time $t + 1$ per individual of stage j at time t , as a function of t , of the environment $E(t)$, and of the population density $\mathbf{n}(t)$.

2.1 What do you get *out* of a demographic model?

1. *Information on the vital rates* (i.e., survival, reproduction, maturation, recruitment, movement) throughout the life cycle:

Estimates and confidence intervals	}	of the vital rates
Trends		
Temporal variability		
Environmental dependence		

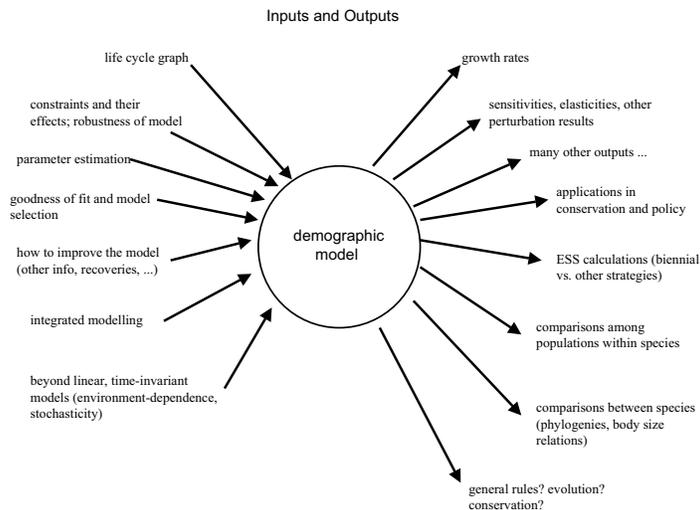


Figure 1: A diagram showing some of the considerations that go into, and some of the results that can be expected to come out of, our demographic modelling efforts.

This subsumes much of what autoecology focuses on: how individual organisms are affected by their environment.

2. *Information on the timing of events in the individual life cycle.* That is, we get the mean, variance, and probability distribution of such things as the time from fledging to recruitment, the interval between breeding events, the time required for recovery after pair disruption.
3. *Population growth, population structure, and reproductive value.* These are the basic components of a description of population dynamics. In a constant environment, where

$$\mathbf{A}[t, E(t), \mathbf{n}(t)] = \mathbf{A} \quad (2)$$

the asymptotic population growth rate is the dominant eigenvalue λ of \mathbf{A} , and the stable stage distribution and reproductive value are the right eigenvector \mathbf{w} and left eigenvector \mathbf{v} corresponding to λ . Transient fluctuations are described by the subdominant eigenvalues.

In a periodic environment (either seasonal or inter-annual), population growth is described by a product

$$\mathbf{A} = \mathbf{B}_p \mathbf{B}_{p-1} \cdots \mathbf{B}_1$$

and everything just said about a constant environment can be applied to this matrix (that is, when viewed on a time scale of its period, a periodic environment is constant).

In a stochastic environment, there is a different projection matrix $\mathbf{A}[t]$ at each time, generated by a process including some degree of randomness. The long-term population growth rate is

$$\log \lambda_s = \lim_{T \rightarrow \infty} \frac{1}{T} \log \|\mathbf{A}_T \mathbf{A}_{T-1} \cdots \mathbf{A}_1\| \quad (3)$$

Environment-dependent models, in which the a_{ij} vary through time because they depend on changes in some environmental factor, have received less attention. They can be analyzed in various ways.

- (a) Given a sequence $E(t)$, one can calculate the corresponding sequence of population growth rates $\lambda(t)$ which show the integrated effect of the environment on all the vital rates.
- (b) If the environmental variable contains a random component (as it probably does), then $E(t)$ can be used to generate a stochastic sequence of matrices that can be analyzed as a stochastic model.
- (c) If $E(t)$ has exhibited trends, LTRE analysis can be used to show how the environment's effect on the vital rates is mapped to population growth rate.
- (d) The environment-dependent model can be used to make projections of population growth corresponding to projected environmental patterns (global warming, etc.)

In a density-dependent model, asymptotic behavior is described not by a growth rate, but in terms of an equilibrium (or other attractor; but this is not likely in seabirds). The equilibrium would be characterized by its response to perturbations (resilience, reactivity) and the population structure.

- 4. *Perturbation analysis, which shows the response of something (often λ) to changes in the parameters* (the vital rates or lower-level parameters determining the vital rates). Those changes might occur because of environmental change, management actions, human activities, or natural selection. The last of these gives a natural connection to evolutionary life history theory, because $\partial\lambda/\partial\theta$ can be interpreted as the selection gradient on the trait θ .
- 5. *Demographic explanations of differences in growth rates.* A comparison of two (or more) times, places, or environmental conditions yields two (or more) population growth rates, say λ_1 and λ_2 . Those rates reflect the differences in all the vital rates, at all the different stages in the life cycle. Each of those differences makes some contribution to the difference in λ , and it is possible to calculate those contributions by writing

$$\lambda_2 - \lambda_1 = \sum_{i,j} (a_{ij}^{(2)} - a_{ij}^{(1)}) \frac{\partial\lambda}{\partial a_{ij}} \quad (4)$$

This technique (called life table response experiment, or LTRE, analysis) makes it possible to assign causation for differences in population rate to particular parts of the life cycle.

- 6. *Evaluation of management tactics.* A management tactic intends to change some of the vital rates. Sensitivity analysis permits calculating the effect on λ of changes in the vital rates that might be caused by one or another management tactic.
- 7. *Persistence, extinction, and quasi-extinction probabilities.* Any demographic model has implications for population persistence. In the simplest models, these implications are simple (the population will persist if $\lambda \geq 1$). In more complex models, they can involve probabilities of quasi-extinction (reduction of the population to a fraction of its current size) or extinction (the disappearance of the last individual).

8. *Projections, long- or short-term.* A demographic model permits projection of future population, according to various scenarios. Projections can be made under hypothetical conditions of

- constancy of the vital rates
- constancy of trends in the vital rates
- constancy of the statistical characteristics of fluctuations in the vital rates
- specified trajectories of environmental variables

If one believes that those hypothetical conditions will actually come to pass, the projection can be used as a prediction, or forecast, of future population growth.

2.2 What goes *into* a demographic model

1. *A description of the life cycle.* Ideally, this description would discriminate between any classes of individuals that differed in survival, reproduction, physiology, or response to the environment. Ideally, all of these stages would be recognizable in the field. In reality, of course, some of the stages cannot be distinguished. Compromises must always be made between including what's important and ignoring what's impossible to measure.
2. *A set of vital rates,* defined by the transitions of individuals possible within this life cycle.
3. *A set of hypotheses about the dependence of the vital rates on time, the environment, and/or density.* These hypotheses define a family of models. The idea that an analysis begins with a family of models making different assumptions, rather than a single model, is now common in the mark-recapture literature, but has yet to filter into the demographic literature.
4. *A set of constraint hypotheses about parameters that cannot be distinguished because some stages are unobservable* (e.g., some parameters set equal to others, or set to fixed values).
5. *Estimates of the parameters of those models* (i.e., estimates of the rates themselves, or of the functional dependence of the rates on time or the environment). Parameter estimates come from several main sources:
 - (a) Multi-stage mark-recapture (MSMR) data which links the parameters explicitly to the structure of the demographic model. MSMR data consist of a set of capture histories. Each capture history records, in each year (or other time interval), whether an individual was seen and, if so, in what state.
 - (b) Census data, recording the number of individuals, in some set of stages or the total population, in each year.
 - (c) External covariate data, recording measurements of one or more variables that might influence the vital rates.
 - (d) Individual covariate data, recording measurements (e.g., of physiological condition) on each individual in each year.
 - (e) Miscellany. It is important to remember that miscellaneous data, perhaps collected for other purposes, may be useful, when we have the ingenuity to use it.

6. *A ranking of those models by how well they are supported by the data* (for example, using AIC or other information-theoretic criteria). Such rankings give different weight to the hypotheses reflected in the models and can be used to create average models.

Part of the ranking process is goodness-of-fit testing, which is still problematic for the models we will be developing, because of the presence of unobservable states.

2.3 From one population to multipopulation comparisons

All the preceding applies to one population. At the next level, analysis of multiple populations, perhaps of several species, opens the possibility of comparative analysis. Such analyses could involve comparisons of

- the vital rates
- the dependence of the vital rates on other parameters
- population growth
- trends in population growth
- variability in population growth
- potential for persistence
- sensitivity and elasticity of population growth (selection pressures, life history theory, management)

We do not know exactly what the possibilities are, because no one has ever attempted a comparative demographic analysis at this level of detail.

3 The Life Cycle

We developed a basic life cycle model based on breeding categories (and including unobservable states) to use as a framework for parameter estimation and demographic analysis. To develop this life cycle, we considered the adult and pre-adult parts of the life cycle separately. This life cycle is an attempt to balance the need for a relatively simple life cycle structure that can be applied across populations for comparative analyses and the need to incorporate important biological features.

3.1 The adult life cycle

Two distinctions seem fundamental: between birds that breed in a given year and those that do not, and of those that breed, between those that succeed and those that fail. For “biennial” breeders, the likelihood of breeding in one year depends on whether breeding in the previous year was a success or a failure.

We arrived at a four-stage adult life cycle, including successful breeders, unsuccessful breeders, post-success non-breeders, and post-failure non-breeders (Figure 2). Figure 2 assumes that adult vital rates depend neither on age (i.e., since birth) or age-in-stage (i.e., since recruitment), but do depend on breeding status and on the success or failure of the most recent breeding attempt.

Many alternatives to Figure 2 are possible:

1. Figure 2 assumes that the vital rates of post-success and post-failure individuals remain distinct until their next breeding attempt. This could be modified by merging post-success and post-failure birds into a single post-reproductive category, after some number of years.
2. Figure 2 assumes that the probabilities of survival, breeding given survival, and success given breeding are independent of the time elapsed since the last breeding attempt. This could be modified by incorporating an age (i.e., time since breeding) structure within the non-breeding categories.
3. Figure 2 does not account for many other factors that are potentially important, e.g. experience, senescence, quality, sex-specific effects or widowling.

The definitions of failure will be important in applying these models, in particular whether birds fail early or late. This may not be clear in the data. Because the non-breeding stages (3 and 4) are unobservable, it is impossible to estimate all the transition probabilities in this model without imposing some constraints. Hunter and Caswell (unpublished) have examined some constraints.

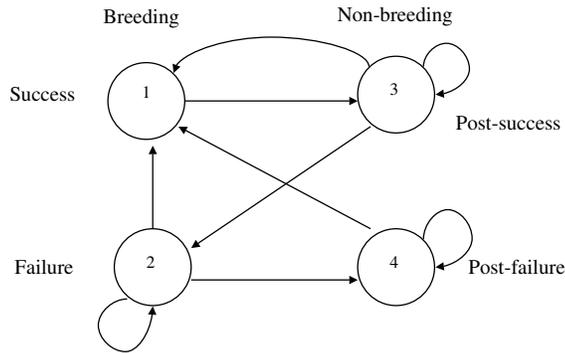


Figure 2: Life cycle graph for the adult portion of the albatross life cycle. As drawn, successful breeders are prohibited from breeding again the next year.

3.2 The juvenile life cycle

The juvenile life cycle encompasses the period from fledging until first breeding. The two main processes are survival and recruitment to breeding. Since only the first stage (fledglings) and the last (breeding adults) are observable, we expect that there will be limits to what can be estimated.

After some discussion, we opted to impose a minimum age at recruitment, as shown in Figure 3. After this minimum age, recruitment might be age-independent or age-dependent. It is difficult to avoid age structure in the juvenile part of the life cycle because of the need to impose a minimum age of first breeding.

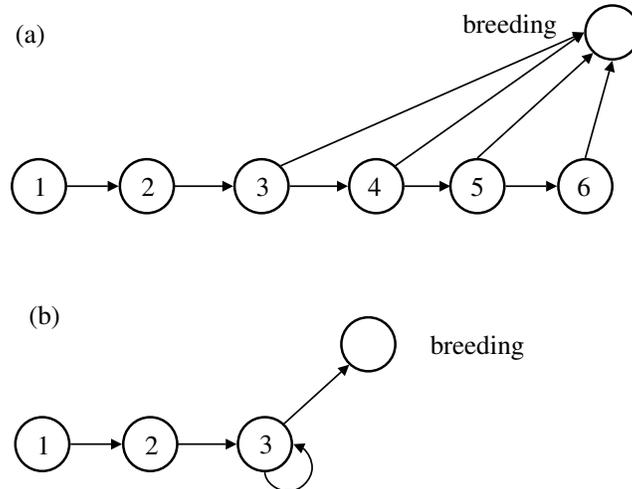


Figure 3: Prototype juvenile life cycle graphs. (a) A graph with a minimum age at recruitment (age class 3 in this case; in reality we used 5 as a minimum in trial analyses of wandering albatross data) and age-specific recruitment probability. (b) The graph simplified by making recruitment and survival age-independent after the minimum age at recruitment.

Many simplifications of Figure 3(a) are possible:

1. We discussed including only a single pre-recruit stage, with age-independent recruitment probability. This got a cool reception, on the grounds that it would fail to capture the actual age schedule of recruitment. This objection depends very much on what criteria are used for comparison; at least two analyses show that population growth rate and the elasticity of growth rate are very robust to such simplifications (Hunter, unpublished, Caswell unpublished).
2. The age-specificity of recruitment can be simplified by assuming a parametric functional form (e.g., logistic) or by creating one or more pre-breeding stages with age-independent recruitment probability.

3.3 The entire life cycle

The entire life cycle (needed for the demographic analysis) is obtained by combining the adult and juvenile portions of the life cycle. The result, in Figure 4, is a basic description of the albatross life cycle. In “biennial” species, the non-breeding categories will have more importance than in non-“biennial” species, but in any species there can be a significant proportion of birds that do not breed in any given year.

Historical note. This life cycle converges surprisingly closely to the life cycle that underlies the wandering albatross model of Croxall et al. (1990). That model was written as a difference equation in the number of breeders, rather than as a matrix model; but there is a close correspondence

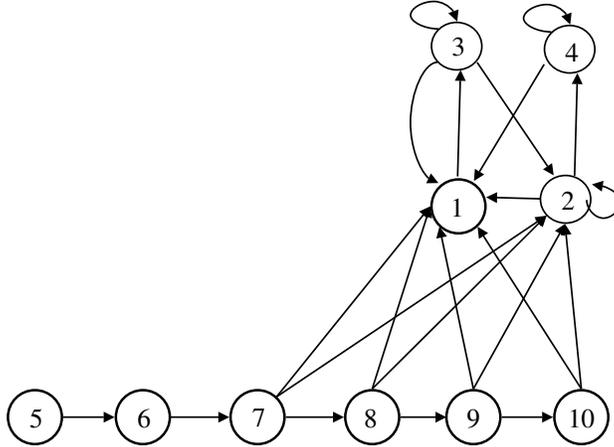


Figure 4: The entire life cycle, obtained by combining the adult life cycle based on breeding state and the juvenile life cycle with age-dependent recruitment.

between these two types of models (Keyfitz 1967). When the Croxall model is translated to a matrix model (MacDonald and Caswell 1993), the corresponding life cycle includes juvenile stages with age-specific maturation probabilities, breeding adults, and post-success and post-failure non-breeders, with different probabilities of return to breeding status. It does not distinguish between successful and failed breeding as states, however.

4 Data preparation

The basic data structure for multistage MR estimation is a set of capture histories, in which the entry for year t represents the stage of the individual in year t if it was captured, or an indication that it was not captured. Additional coding might include specification of unknown states and recovery of dead individuals. (Data sets might also include information on individual covariates, external covariates, or population size; these will be explored at future meetings.) To go from original database records to a set of capture histories requires careful data coding; this coding will be important to the validity of comparisons among species and populations.

We transformed two wandering albatross data sets (BAS and CNRS) and the Buller’s albatross data (Sagar) into an appropriate form for a multi-stage mark-recapture analysis (MSMR). In so doing, we identified questions about how the data is coded and developed recommendations for further coding. Copies of the data sheets are included in the Appendices.

4.1 Data coding

BAS wandering albatross data set Two subsets of the data were created. One contained females only of known age from 1980 to 2003 (2838 recapture histories). The second contained females, males and unknown sex birds (mostly fledglings that never returned as breeders) ringed as

fledglings from 1980 to 2003 (9196 recapture histories). Information is also available on recaptures of fledglings that do not attempt to breed, and recapture of breeding birds that do not attempt to breed.

Categories delineated in the BAS wandering albatross data set:

- fledgling
- successful breeder
- failed breeder

Buller's data set This data set contained only females, only recapture histories after 1992 (data are inconsistent prior to this), all colonies were combined, breeding bird and known-age data sets were combined.

Categories delineated in the Buller's data set:

- bird breeding successfully
- bird breeding unsuccessfully
- bird present on colony but apparently not breeding
- bird breeding for the 1st time, unsuccessfully
- bird breeding for the 1st time, successfully

Questions and issues related to data coding

1. Precise definitions of states will be needed for consistency in coding data from different data sets. Definitions of breeding failure will be particularly important.
2. For data sets distinguishing between males and females we need to be aware of biases induced by being unable to sex birds before they breed. If birds that don't survive or don't breed are eliminated, this eliminates birds with low survival. We need to carefully consider how to treat birds of unknown sex?
3. How to treat records of birds (pre-breeders or birds that have previously bred) present at the colony but not breeding. Should these be classified as not breeding, failed, or not seen?
4. How to treat known versus unknown age birds?
5. How are colonies combined?
6. How to treat situations where data collection methods were inconsistent over time?
7. If both sexes are included, do we need to treat pairs as non-independent?

8. What checks need to be made in the data. For example, should 1's followed by 1's or 1's followed by 2's be assumed to be errors and removed from the data.
9. Is information available on whether a breeding attempt failed early or late.

5 Estimation Procedures

Estimation is simple in principle, but challenging in practice, especially when the model includes unobservable states. Classical capture-recapture models rely on several assumptions regarding independence of individuals and homogeneity of recapture or survival probability among individuals (after accounting for some specific sources of variation). Violations of these assumptions may require adjustments to the model structure or correction for overdispersion.

5.1 Constraints and parameter estimability

The need to impose constraints to render the models estimable will be a major challenge for the group. Although Jaume, Christine, and Hal have tabulated some results about parameter estimability for models of some parts of the life cycle, it is not clear how alternate choices of constraints will affect the results, or how to interpret such effects. We found at the workshop that different constraints applied to the same model may produce the same deviance. JDL described this as the estimates from maximizing the likelihood falling along a ridge; there is no clear way to distinguish one set of estimates as being better than the other. External variables may provide a way to distinguish among estimates. Possible alternatives include integrated modelling, expert opinion, recovery data, other? This is likely to be an important topic for the next meeting. We will need to create a list of the external information available for each data set, e.g. census, immigration, recoveries. Each list needs to be prioritized in terms of what is expected to be most efficient (to provide the greatest information) and for what reason. Some model outputs other than population growth rate are less sensitive to adult survival so more robust to this.

5.2 Estimation platforms

Various people attempted running versions of the models in the three primary platforms for MSMR estimation: MARK, M-Surge and Matlab. M-Surge is fast (when driven by someone familiar with it) and direct, especially if you choose not to calculate confidence intervals. Routines in the Matlab Optimization Toolbox can be used with matrix formulations of MSMR estimation to generate estimates in cases that M-Surge is not designed to handle (e.g. parameterization in terms of lower-level parameters), but is much slower and requires coding for each use. We had little success in getting even simple versions of the models (Figures 2-4) to converge in MARK.

5.3 Model selection

Model selection works the same as for single state models. A candidate model set is defined based on a priori biological hypotheses (considering all the possible models corresponding to simplifications of the general one is unlikely to be practical or desirable). Candidate models are compared using Akaike's Information Criteria (AIC or AIC_c -adjusted for small sample sizes). This is reliable given that at least one model fits the data reasonably well (Burnham and Anderson 2002). Akaike

weights, w_i , reflect the relative support for each of the models in the model set. The weight, w_i for model i can be interpreted loosely as the weight of evidence in favor of that model being the most appropriate, given the data and given the model set. The relative importance of each parameter can be assessed by summing Akaike weights across all models containing the given parameter.

Model selection procedures based on information criteria permit consideration of a set of models whose structure reflects specific biological hypotheses that are not necessarily exclusive or alternative. Comparisons among models permits assessment of these hypotheses, even if the corresponding models are not nested (which would preclude the use of test statistics such as likelihood ratio tests).

A few issues that we need to keep in mind

- We need to be aware that trends may be the result of heterogeneity.
- We need to address the issue of band loss.
- It would be useful to make comparisons of naive vs state-of-the-art estimates to be able to make retrospective comparisons with previous approaches.
- We need to consider whether extra assumptions will be required for 2-sex models - and whether this changes the variables we should be estimating?

5.4 Goodness-of-fit

Goodness of fit is an important but difficult issue because currently known methods do not apply (or do not apply easily) to multistate data with unobservable states (i.e. the kinds of models we are trying to fit). Some approaches, such as the goodness-of-fit test to the Cormack-Jolly-Seber model (which is based on contingency tables), are specific to a given model. Others rely on an overdispersion parameter computed by means of bootstrap procedures (and can be applied more generally). While the latter are more general, they do not distinguish between structural failure and overdispersion, and their reliability for multistate models is not well established.

JDL offered to work with Roger Pradel to develop a protocol for goodness-of-fit tests for the general life cycle model and to estimate \hat{c} using the BAS wandering albatross data set as an example. The goodness-of-fit test will require a generalization of the single state case (see Pradel R., C.M.A. Wintrebert and O Gimenez. 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. *Biometrics* 59:43-53.). Issues related to sparseness of data are likely to arise.

Deviance is inflated to an unknown degree when none of the models fit the data. Another possibility is to run the model without any of the unknown states, then using the \hat{c} value derived from that model to adjust the deviance for the models with observable states (see Euring 2000 proceedings, \hat{c} from single state reduction of data - *Oikos*). This will be conservative, because \hat{c} will be bigger than the actual lack of fit. It will be good practice to check the profile likelihood for the final model to make sure there aren't flat areas.

6 A Wandering Albatross Example

We spent considerable time grappling with M-Surge, Matlab, and MARK, trying to obtain parameter estimates. None of those attempts were based on a complete data set (or even a completely

trustworthy implementation of a subset), and none were free of doubts about convergence and identifiability. But here is an example, for the wandering albatross, estimated using a life cycle like Figure 4. Stages 1–4 are adults; stages 5–12 are juveniles (stage 5 being 1 year old). The earliest breeding happens in age-class 5 (stage 9). Breeding propensities differ for age classes 5–8 (stages 9–12). All individuals in age class 8 that survive return to age class 8.

The transition matrix Φ is

$$\Phi = \left(\begin{array}{cccc|cccccccc} 0 & 0.455 & 0.642 & 0.719 & 0 & 0 & 0 & 0 & 0.001 & 0.014 & 0.083 & 0.182 \\ 0 & 0.360 & 0.289 & 0.232 & 0 & 0 & 0 & 0 & 0.002 & 0.024 & 0.128 & 0.237 \\ 0.914 & 0 & 0.022 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.100 & 0 & 0.000 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ \hline 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.866 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.952 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0.952 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.952 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.950 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.914 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0.741 & 0.532 \end{array} \right) \quad (5)$$

The projection matrix \mathbf{A} is obtained by including reproduction, into this matrix. There are two ways (at least) of doing this, which we will denote here as the *HC Method* and la *Méthode JDL*.

The HC method Define a fertility matrix \mathbf{F} , whose $(5, j)$ entry ($\phi_{1,j}$) is the fertility of stage j .

This fertility is the number of new fledglings (stage 5 in this life cycle) at time $t + 1$ per individual in stage j at time t . Any time an individual enters the successful breeding stage (stage 1), it produces a fledgling (that is the definition of success). Assuming an even sex ratio at birth, this would mean that

$$f_{5,j} = 0.5\phi_{1,j} \quad j = 1, \dots, 12 \quad (6)$$

La Méthode JDL A successful breeder at time t is a bird who has just begun the breeding process. Since it is successful, this means that it will have a surviving fledgling at $t + 1$. Thus the fertility matrix has only a single positive entry,

$$f_{5,1} = 0.5 \quad (7)$$

The difference between these two approaches depends on timing. The HC method is a pre-breeding census formulation of the matrix. It considers a successful breeder (i.e., a bird observed in stage 1) to be sitting with a fat and happy fledgling at the end of its breeding season. La méthode JDL is a post-breeding census formulation. It considers a successful breeder to be at the beginning of its breeding event, laying an egg. The bird doesn't know that it will be successful, but we, armed with hindsight, do. Thus it will produce a fledgling one year later. *Choosing the appropriate method will require careful consideration of how the data are defined*, which in turn affects the definitions of the stages in the model. The sense of the discussion was that the structure of the BAS and Buller's data sets correspond more closely to a post-breeding census.

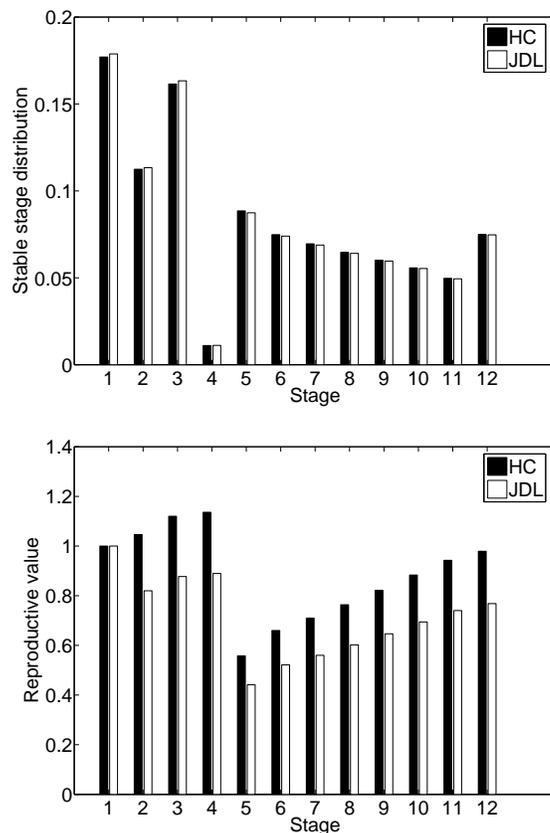


Figure 5: Stable stage and reproductive value distributions for the wandering albatross model, according to the HC and JDL methods of incorporating fertility.

The differences in the results for the HC and JDL models that we calculated during the workshop and report here result from slightly different treatments of survival. Pre- and post-breeding formulations will usually give the same population growth rate.

	HC	JDL
population growth rate	1.0242	1.0229
damping ratio	1.3194	1.2527
period of oscillation	11.9731	13.1083

The entire eigenvalue spectra of the two models are very similar. So are the stable stage distributions, with about 46% of the population adults (stages 1–4), and of those about 62% breeding in any year. Overall, the breeding population (both successful and failures) represents about 29% of the total population (Figure 5). The reproductive value schedules are somewhat different, although the patterns are very similar (Figure 5). Sensitivity and elasticity of λ to the matrix entries behave as expected, and are hardly affected by the choice of a fertility model (Figure 6).

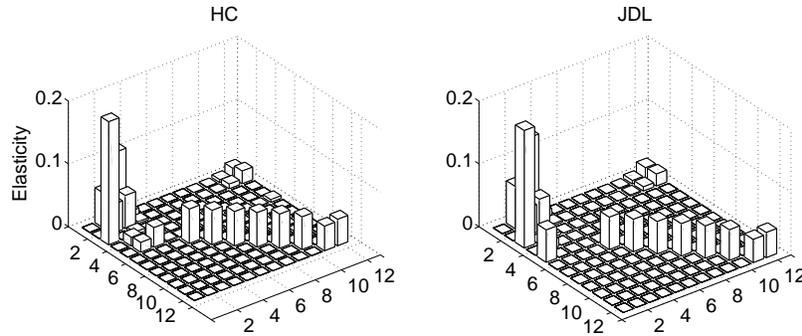


Figure 6: Elasticity matrices for the wandering albatross model, according to the HC and JDL methods of incorporating fertility.

The transition matrix Φ gives information on the breeding interval (Caswell, unpublished). For example, here are some mean intervals (in years), conditional on eventually breeding:

From:	
fledgling to first success	9.46
fledgling to first breeding	8.49
success to next success	2.52
success to next breeding	2.02
post-success to next success	1.79
post-success to next breeding	1.11
post-failure to next success	1.52
post-failure to next breeding	1.00

where “next breeding” means either success or failure. Other than noting that the values are not unreasonable, nothing much should be made of these results yet.

7 Next Steps

An important part of the meeting was discussions on how to proceed. To obtain reliable estimates of survival and transition rates we will need address issues related to data coding, goodness-of-fit and model selection. Several side issues related to estimability, the use of constraints, and effects of model mis-specification will also need to be investigated.

The following list of steps was suggested.

1. We have a basic life cycle model, and it appears that the parameters can be estimated, at least sometimes. To use that model, we need to:

- (a) Revisit data preparation procedures - define categories, make decisions about data treatment, and partition data sets more precisely. Many of these issues will be population-specific. The goal is to produce data files with the organization we need and to achieve as much consistency in data treatment among data sets as possible.
 - (b) Transform data (for each of the data sets people wish to include) into capture histories coded so that they can be numbered to correspond to stages in the basic life cycle (or other models we may come up with).
 - (c) Generate parameter estimates for each data set (adjusting the model if necessary).
2. The parameter estimation process presents some methodological challenges. Some of these may be long-term projects, but we should at least begin to:
 - (a) Investigate the effects of the constraints required to make parameters identifiable.
 - (b) Develop profile likelihood methods for model comparison.
 - (c) Work on the goodness-of-fit problem.
 3. We should also begin to think about moving beyond the basic model we considered here. That involves:
 - (a) Create a list of extra information available for each data set (e.g., census data, recovery data).
 - (b) List environmental factors that may be used as covariates.

We hope (this should not be too optimistic) that some of these items can be achieved before the next meeting, particularly steps 1a and b.

8 Goals For the Next Meeting

Our goals for the next meeting are to progress further on the parameter estimation, if possible working with complete and finalized data sets. We will also have presentations/discussions aimed at specific aspects of the analysis such as goodness-of-fit, model selection, and addition of covariates. We hope to tackle the following:

- Fit models to data sets we trust, for as many populations as possible. This includes goodness-of-fit testing, model selection,
- Begin to investigate covariates. A lot of interest was expressed in examining the effects of covariates, particularly environmental variables. Potential covariates include pair status (e.g. mate loss, repair, divorce), environment (SST, sea ice extent, SOI), fisheries impact, and effort.
- Investigate use of additional data (e.g. census data using integrated modelling, data on pairs as info on survival)
- Discuss what questions to address next - e.g. how to improve the life cycle model to account for senescence, widowhood, other factors?

- Conduct a first round of demographic analyses
- Investigate how these data and the process can be used to inform new kinds of theory and theoretical models (e.g. persistent pair bonds)

We realize this will be an ambitious agenda.

Appendix A: Participants

Table 1: Participants of the Albatross Demography Working Group

Present at First Meeting, September 20-26, 2004 WHOI	
Niall Broekhuizen	Christchurch, New Zealand
Hal Caswell	WHOI
Paul Doherty	Fort Collins, Colorado
Jaume Forcada	Cambridge, England
Christine Hunter	WHOI
JD Lebreton	Montpellier, France
Mike Neubert	WHOI
Paul Scofield	Christchurch, New Zealand
Sophie Veran	Montpellier, France
Stephanie Jenouvrier	Chize, France
Unable to Attend First meeting, September 20-26, 2004 WHOI	
John Croxall	Cambridge, England
Rosemary Gales	Tasmania, Australia
Jim Nichols	Baltimore, Maryland
CJR Robertson	Wellington, New Zealand
Michael Runge	Baltimore, Maryland
Peter Ryan	Cape Town, South Africa
Paul Sagar	Christchurch, New Zealand
Henri Weimerskirch	Chize, France

Appendix B: Questions of Interest

The following list of questions was created during a brainstorming session. The aim was to elicit the type and scope of questions people were interested in addressing. This list represents questions that individuals, small groups or the group as a whole could address. This list is intended to stimulate discussion and ideas and to provide a context within which we can decide which direction to go, what order to progress in. This list is not intended to cover all the possible questions that we either could, or that we intend to, address.

1. Age, Quality and Density Related Questions

- (a) Does age at first breeding predict long-term breeding success (is it a quality indicator)?
- (b) Is there assortative mating by age?
- (c) What are measures of delayed reproduction?
- (d) Do albatross exhibit senescence? Is this reflected in increased skipping, increased mortality, or other factors?
- (e) Is there age-dependence of skipping? What are the effects on estimates of growth rate?
- (f) How important is individual heterogeneity (in reproduction or survival)?
- (g) Is there any evidence of density-dependence in recruitment (territory limitation or quality)?
- (h) Is there any evidence for density-dependence in survival?
- (i) Is there evidence of biased sex ratios - chicks produced or recruited breeders?
- (j) What environmental factors are important for reproduction and survival?

2. Widowing/Re-Pairing and Breeding Related Questions

- (a) What are the consequences of sexual segregation in feeding/mortality?
- (b) Are there male and female behavioral differences?
- (c) What are the consequences of using female dominant models?
- (d) What are the consequences of widowing and re-pairing (will lambda always be biased high)? Are there differential
- (e) effects of widowing by sex/age?
- (f) Can we develop 2-sex models to account for male-biased catch in fisheries?
- (g) Two sex models in general
- (h) Are there extra assumptions for 2-sex models and does this change the variables we should be estimating?

3. Space And Time Scale Questions

- (a) What are the medium to long-term effects of single demographic events, e.g. breeding failure events?
- (b) Are there delays in detecting population decreases? What are the consequences?

- (c) What are the effects of differences in time scale between management/monitoring (time lags) and population impacts?
 - (d) What are important timing variables - e.g. birth interval, age at recruitment, generation time?
 - (e) Can we develop ad hoc rules of thumb for maximum growth rate?
 - (f) How can we best account for dispersal - can we link to gene flow and genetic studies?
4. Evolutionary Questions
- (a) Why do albatrosses lay one egg?
 - (b) Why is reproduction delayed? Is this related to scale - distance to feeding etc.?
5. Stochasticity
- (a) Do albatross life cycles buffer against stochasticity?
 - (b) Is it common to have small effects of demographic and environmental stochasticity?
 - (c) How is reproduction versus survival used in 'buffering' stochasticity?
 - (d) Should we use random effects to estimate process variance?
6. Management Questions
- (a) How to design a study (could we produce a paper on this)?
 - (b) Suggestions for improvement for ongoing studies?
 - (c) What are the effects of and how much take can be tolerated?
 - (d) How do you use demographic models to say how much mortality is OK?
7. Technical Questions/Issues
- (a) Can we use random effects estimation for stochastic matrix models?
 - (b) How do we estimate band loss?
 - (c) Use of robust design
 - (d) What is the optimal allocation of effort to banding, telemetry, and monitoring effort in general?
 - (e) How to estimate survival for biennial breeders (how to account for temporary emigration)?
 - (f) How do you model average over different life cycles (super models)?
 - (g) What is the best way to average over demographic models?
 - (h) What is the best way to combine data from differing species/populations (also dispersal)?
 - (i) Are there new technologies we can make use of, e.g. age estimation from bones?
 - (j) List of future directions for statistical developments (MR) etc. to ensure future data is useful.
 - (k) How robust are estimates compared to naive approaches?

- (l) What are the effects of using different constraints to make the models estimable?
- (m) How can these data and the process be used to inform new kinds of theory and theoretical models (e.g. persistent pair bonds)

8. Comparative Questions

- (a) Is there synchrony among populations or species?
- (b) How do annual and biennial species differ?
- (c) Are *Phoebastria* more subject to more variation in breeding proportions than other sp?
- (d) How do we account for space/time scale issues (e.g. feeding) in comparative analyses?
- (e) Can we establish rules of thumb for population growth rate, take etc..

Appendix C: Buller's Data Sheet

Procedures used to encode Buller's Albatross Data for the First Albatross Demography workshop, Woods Hole, September 20-26, 2004.

Species: Buller's albatross (*Thalassarche bulleri*)

Geographic locations: Snares Island and Solander Island, New Zealand

Period: 1972-2004?

Data: Breeding birds and known-age birds

Coding used for the breeding bird data set from main study colony:

1. bird present on colony but apparently not breeding
2. bird breeding unsuccessfully for 1st time
3. bird breeding successfully for 1st time
4. bird breeding unsuccessfully
5. bird breeding successfully

Table 2: Breeding bird data from the main study colonies was supplied in the following format:

Band	Sex	Colony	Banded	1992	1993	1994	...	2003	2004	Male	Female
31456	F	LPB	1972	5	5	5	...	5	4	0	1
47558	F	MB	1994	0	0	0	...	2	5	0	1

These data include an extra layer of data regarding 21 known age birds that began breeding during the study.

Coding used for the known age data set from all colonies:

1. bird present on colony

Table 3: Known age data from all colonies was supplied in the following format:

Band	Sex	1992	1993	1994	...	2001	2002	2003	2004	Breeding?
54171	F	1	0	0	...	1	1	1	1	Breeding 2001, 2003, 2004
54408	F	1	0	0	...	1	0	0	1	Breeding 2001, 2004
54285	F	1	0	0	...	0	1	0	0	Breeding 2002
54105	F	1	0	0	...	0	1	1	0	
54148	F	1	0	0	...	1	1	1	0	

Note: Bird 47558 was banded as a chick in 1994 (these Individuals can be recognized as no number is included in the 1994 column but it is indicated that the bird was banded in 1994).

Formatting Data for Multi-stage Mark-Recapture Analyses To conform with the data encoding used to formulate a multistage mark-recapture format we modified the dataset using these methods:

1. Only females were analyzed in this analysis
2. All recapture histories before 1992 are ignored as data were not collected consistently
3. All colonies were considered to be similar and thus combined
4. The breeding bird data set and the known age data set from all colonies were combined and the 21 replicated individuals were not erased.
5. Chick banding year was interpolated (using the explanation above) and the year of fledgling given the
6. Category 5 in the original data set became 1 = Successful breeder (S)
7. Category 4 in the original data set became 2 = Unsuccessful breeder (F)
8. All Category 1 recaptures from the breeding bird data from main study colony were considered to be 0. Category 1 recaptures from the known age data from all colonies were considered to be 1 = Successful breeder (S) if the final column indicated that they had bred that year otherwise all recoveries were considered to be 0.

Additional data that exists and should be included in future analysis

- Whether an individual failed early or late

Appendix D: British Antarctic Survey Wandering Albatross Data Sheet

Data from the British Antarctic Survey provided for the First Albatross Demography Workshop, Woods Hole, September 20-26, 2004.

Species: wandering albatross (*Diomedea exulans*)

Geographic location: Bird Island, South Georgia

Period: 1980-2003

States

- fledglings (code 5)
- successful breeders (code 1)
- failed breeders (code 2)

Release-recapture information:

1. Release of birds ringed as fledglings
2. Recapture of fledglings returning as pre-breeders
3. Recapture of breeding birds as successful breeders
4. Recapture of breeding birds as failed breeders
5. Recapture of breeding birds which do not attempt breeding

Definitions:

- fledgling: bird about to leave the island at the end of the breeding season
- pre-breeder: bird ringed as fledgling that has never been seen before attempting breeding on the island
- successful breeder: bird which attempts breeding and whose chick fledges
- failed breeder: bird which attempts breeding and whose chick dies before fledging
- non-breeder: bird that has bred before and is observed at the colony but does not attempt breeding; i.e. does not pair or sit in a nest. (These are birds who potentially have lost a pair or have "divorced").

Potential covariates:

- mate loss, repair, divorce

- environment (SST, ice extent)
- fisheries impact

The data may also be grouped by sex or by pair.

Subsets of the data used for preliminary analyses during the workshop

1. Breeding histories of females of known age from 1980 to 2003, which total 2838 recapture histories. (example format 0000010122210102)
2. Annual cohorts of known age birds (ringed as fledglings) from 1980 to 2003 which total 9196 recapture histories, with females, males and unknown birds (mostly fledglings that never return as breeders) grouped together. (example format 55000001012221010)

Data cleaning

- eliminated 1's followed by 1's or 2's (assumed to be errors).
- eliminated sightings of pre-breeders prior to the first breeding attempt.

Only ringed fledglings from 198? on so need to be aware of age effects in the data.