

The Jolly-Seber model: more than just abundance

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Abstract

The Jolly-Seber model provides estimates of abundance, survival, and capture rates from capture-recapture experiments. This paper will describe recent extensions to the following cases: (a) multiple-cohort studies where recruitment rates are compared among cohorts; (b) age-specific breeding proportions; (c) population growth rates. Finally, new areas of research needed for this model are proposed.

Keywords: animal abundance; breeding proportions; capture-recapture; Cormack-Jolly-Seber; Jolly-Seber; mark-recapture; survival estimation;

1 Introduction

It is now just over 40 years since Darroch (1959) developed models for capture-recapture experiments on populations with either immigration or death (but not both). Six years later both Jolly (1965) and Seber (1965) derived both estimators and variances for the general case.

Since that time, extensive work has been done on capture-recapture models with Seber (1982), Seber (1986), Seber (1992) and Schwarz and Seber

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(1999) providing extensive reviews. Work in this field can be broadly divided into three areas: closed population models; models following marked animals over time allowing only survival (and not recruitment) estimation – the Cormack-Jolly-Seber (CJS) models (Cormack, 1964; Jolly, 1965; Seber, 1965); and fully open population models allowing for estimation of both recruitment and survival – the Jolly-Seber (JS) model (Jolly, 1965; Seber, 1965).

Development of methods for closed populations has been extensive and beyond the scope of this paper.

Many developments of models for the Cormack-Jolly-Seber approach have also occurred. Lebreton et al. (1992) extended the method to multiple groups in an ANOVA-type framework. Schwarz, Schweigert, and Arnason (1993), and Brownie et al. (1993) introduced movement models. Burnham (1993) and Barker (1997) showed how to combine recaptures, resightings, and returns of dead animals. Powerful software (*MARK* by White and Burnham, 1999; *SURGE* by Pradel and Lebreton, 1991) has been developed to assist in model fitting and selection. In all of these approaches, emphasis has been placed on modeling survival rates. Because only marked animals are followed over time, no estimates of abundance are available.

Surprisingly, much less work has been done on Jolly-Seber models where abundance estimation is also possible. Part of the reason is related to experimental design issues. The experimental protocol needed to successfully follow only marked animals over time is much less rigorous than that needed to also model the introduction of new unmarked animals into the population. In recent years, there have been a resurgence of interest in the JS model focusing on more than simple abundance.

This paper will review and summarize three recent developments in the JS model that move the emphasis away from survival and abundance estimation. These are:

- modeling the pattern of entrance of new recruits. This required the development of a new likelihood function.
- modeling age-specific breeding proportions. Clobert et al. (1994) used the CJS framework for this, but a more natural framework is a modification of the JS model.
- modeling population growth, dilution or fecundity. Pradel (1996) and Pradel et al. (1997) used the CJS framework on reversed capture-histories, but again these quantities fall naturally out of the JS model.

Finally, I speculate on where future research work on the JS model is

needed.

2 Notation

The notation for JS models has been relatively standardized and follows to a great extent that of the CJS model. Sample occasions are usually denoted by the subscript i while group membership is denoted by the subscript g . The experiment has k sample occasions.

“Birth” refers to any mechanism by which new animals are added at unknown times to the catchable population (by immigration, reproductive recruitment, etc.). Similarly, “death” refers to all processes that permanently remove animals from the catchable population (permanent emigration, death, etc.). We do not distinguish between sources of new animals or between the ways animals leave the population. Births at known sample times (e.g. by deliberate addition of marked animals) are called injections and deaths at known sample times are called losses on capture.

Statistics:

- n_{gi} total number from group g captured at sample time i .
- m_{gi} total number of marked animals from group g captured at sample time i .
- u_{gi} total number of unmarked animals from group g captured at sample time i .
- R_{gi} number of animals from group g that are released after the i^{th} sample. R_{gi} need not equal n_{gi} if losses on capture or injections of new animals occur at sample time i .
- r_{gi} number of the R_{gi} animals released at sample time i that are recaptured after time i .
- z_{gi} number of animals from group g captured before time i , not captured at time i , and captured after time i .

Fundamental Parameters:

- p_{gi} probability of capture for animals in group g at sample time i .
- ϕ_{gi} probability of an animal from group g surviving and remaining in the population between sample times i and $i + 1$, given it was alive and in the population at sample time i .
- N_g total number of animals in group g that enter the system and survive until the next sample time. $N_g = B_{g0} + B_{g1} + \dots + B_{g,k-1}$.
- β_{gi} fraction of the total net births that enter the system between sample times i and $i + 1$. These are the entry probabilities. $\beta_{gi} = B_{gi}/N_g$.

Functions of parameters:

- B_{gi} number of animals of group g that enter after sample time i and survive to sample time $i + 1$. The B_{gi} are referred to as the net births. B_{g0} is defined as the number of animals alive just prior to the first sample time.
- λ_{gi} population growth rate for group g between sample times i and $i + 1$.
- f_{gi} the fecundity rate for group g between sample times i and $i + 1$.
- γ_{gi} the seniority probability or the probability that an animal present just before time i was already present just after time $i - 1$. $\gamma_{gi} = \frac{N_{g,i-1}^+ \phi_{g,i-1}}{N_{gi}^-}$
- ψ_{gi} probability that an animal enters the population, is still alive, and is not seen before time i . $\psi_{g1} = \beta_{g0}$, $\psi_{g,i+1} = \psi_{gi}(1 - p_{gi})\phi_{gi} + \beta_{gi}$.
- N_{gi} population size for group g at time i . $N_{g1} = B_{g0}$, $N_{g,i+1} = (N_{gi} - n_{gi} + R_{gi})\phi_{gi} + B_{gi}$.
- U_{gi} number of unmarked animals in group g in the population at time i . $U_{g1} = N_{g1}$; $U_{g,i+1} = U_{gi}(1 - p_{gi})\phi_{gi} + B_{gi}$.

3 Modeling the pattern of recruitment

Lebreton et al. (1992) developed methods to compare survival and catchability among groups of animals, e.g. to compare the survival rates of males and females across time?

In the JS model, rather than comparing raw abundance among groups, the relative increase or pattern of increase may be more interesting, e.g. to see whether the pattern of recruitment is the same for males and females?

The impediment to a parallel theory of Lebreton et al. (1992) for JS models was the lack of a suitable parameterization and likelihood function. Starting with Darroch (1959), it has been well known that the full likelihood for a JS capture-recapture experiment can be partitioned into three components, $L = L_1 \times L_2 \times L_3 = P(\text{first capture}) \times P(\text{releases}|\text{captures}) \times P(\text{recaptures}|\text{captures})$. The latter two components can be modeled by products of conditionally independent binomial distributions as shown by Brownie et al. (1985) and Burnham (1991), and are now the standard representation. There is no such accepted standard for L_1 . Indeed, the most convenient form depends upon what is to be estimated.

Darroch (1959) derived the likelihood function for L_1 in the case of immigration or death (but not both). He treated the B_{gi} as fixed constants and noted that L_1 involved $(k - 1)$ dimensional sums of probabilities making its maximization intractable.

Jolly (1965) and Seber (1965) assumed that U_{gi} are fixed parameters. Then, by defining $B_{gi} = U_{g,i+1} - \phi_{gi}(U_{gi} - u_{gi})$, L_1 can be written as a

product of binomials:

$$L_1 = \prod_{g=1}^G \prod_{i=1}^k \binom{U_{gi}}{u_{gi}} (p_{gi})^{u_{gi}} (1 - p_{gi})^{U_{gi} - u_{gi}}$$

with the maximum likelihood estimators of U_{gi} being $\hat{U}_{gi} = u_{gi}/\hat{p}_{gi}$.

There are several problems with this approach. First, ‘births’ do not explicitly enter in the likelihood, which makes it difficult to impose constraints upon the B_{gi} such as being zero at certain times, or being equal among groups at a particular time, or being a function of covariates. And the likelihood models the raw counts; translating these to a pattern of recruitment was not feasible making modeling along the lines of Lebreton et al. (1992) extremely difficult. There are also some technical difficulties as outlined by Schwarz and Arnason (1996).

This was the commonly accepted formulation until the mid-90’s. Cormack (1989) and Burnham (1991) derived alternate representations, but these were not entirely satisfactory.

Over 30 years after Jolly (1965) and Seber (1965), Schwarz and Arnason (1996) built upon the work of Crosbie and Manly (1985) to develop a formulation that resolved a number of issues. They treated $B_{g0}, \dots, B_{g,k-1}$ as random variables conditional upon N_g (the total number of unique animals in the experiment in group g), and let $\beta_{g0}, \dots, \beta_{g,k-1}$ be the fraction of the population that entered between sampling occasions i and $i + 1$ and survived to the next sampling occasion. Then $B_{g0}, \dots, B_{g,k-1}$ follow a multinomial distribution, leading to

$$L_1 = \prod_{g=1}^G \binom{N_g}{u_g} \left(\sum_{i=1}^k \psi_{gi} p_{gi} \right)^{u_g} \left(1 - \sum_{i=1}^k \psi_{gi} p_{gi} \right)^{N_g - u_g} \times \binom{u_g}{u_{g1}, u_{g2}, \dots, u_{gk}} \prod_{i=1}^k \left(\frac{\psi_{gi} p_{gi}}{\sum_{i=1}^k \psi_{gi} p_{gi}} \right)^{u_{gi}}$$

Here $\{\psi_{gi}\}$ is a function of the relative birth rates $\{\beta_{gi}\}$. The likelihood can now be expressed as a product of multinomial and binomial distributions in much the same way as was done for the CJS model.

The new formulation leads to all the usual estimators of Jolly (1965) and Seber (1965). Because the parameters describing the ‘birth’ process are directly available in the likelihood, it is relatively easy to selectively constrain subsets to be zero, to be equal over time, to be equal among groups, or to be functions of covariates. All the machinery developed for model selection (likelihood ratio tests and AIC) for the CJS models can be used directly. The computer package *POPAN* (Arnason, Schwarz, and Boyer, 1998) implements all of these modifications to the JS models.

Parameterizing in terms of the *proportions* of new animals that enter between sampling occasions is also advantageous. First, it would be quite unusual when conducting an experiment on two groups of animals whose absolute population sizes could be quite different to expect that the absolute recruitment would be equal for the two groups. However, the pattern of recruitment may be equal. Schwarz and Arnason (1996) presented such an example of salmon returning to spawn where sampling occurred weekly. Returning salmon can be classified into two groups: adults that returned at age 3; and jacks which are precocious males returning at age 2. A question of interest is whether the two types of males return in the same pattern. Extending the notation of Lebreton et al. (1992), Schwarz and Arnason (1996) used AIC to select the model $\{p_g, \phi_t, \beta_{g*t}\}$ as the most suitable and the estimates are shown in Table 1. This shows that adults and jacks had unequal catchability, had similar survival patterns over time, but more importantly, the pattern of returns for the two groups was different with jacks tending to return earlier than adults.

Second, estimates of $\{\beta_{gi}\}$ are relatively free of the biases caused by heterogeneity in catchability. Carothers (1973) showed that the asymptotic relative bias of \hat{N}_{gi} is a function of the γ_{gi} , the coefficient of variation in the capture-probabilities, because $E[\hat{N}_{gi}] \approx N_{gi}/(1 + \gamma_{gi}^2)$ but that survival estimates are essentially unaffected by heterogeneity. If the coefficient of variation in catchability is relatively constant over time, then both

$$\hat{B}_{gi} \approx \hat{N}_{g,i+1} - \hat{N}_{gi}\hat{\phi}_{gi}$$

and $\hat{N}_g = \sum_{i=0}^{k-1} \hat{B}_{gi}$ have the same relative bias, but $\hat{\beta}_{gi} = \frac{\hat{B}_{gi}}{\hat{N}_g}$ will be relatively free of bias. This has been confirmed by the author using methods similar to Carothers (1973) and in simulation studies. Hence, it may not be necessary to use methods such as Pledger and Efford (1998) to try to correct for heterogeneity in these cases.

Because the $\{\hat{\beta}_{gi}\}$ are relatively free of bias caused by heterogeneity in catchability, it implies that estimators based on these should also be relatively unaffected. For example, Manske and Schwarz (2000) developed an estimator for stream residence of fish from JS experiments that is insensitive to heterogeneity in catchability.

4 Age-specific breeding proportions

Clobert et al. (1994) used the CJS model to estimate age-specific breeding probabilities from studies of successive cohorts of animals marked as young.

The difficulty in fitting a standard CJS model to these data is that the marked animals in a cohort after breeding has commenced but before all animals have become breeders, consist of two subgroups – those who are non-breeders, which cannot be observed and those who are breeders, which can be recaptured. This heterogeneity in the capture probabilities violates a key assumption of the CJS model that all animals alive have the same probability of recapture at a sampling occasion. Clobert et al. (1994) introduced a number of parameters representing the overall, average, probability of capture during the progression to full breeding status, and it was the changes in these values that allowed them to estimate the breeding probabilities.

Because it is changes in the average probabilities of capture that lead to estimates of the breeding proportions, it is difficult to numerically constrain these to be positive, or to test for equality of these parameters among groups, or to model them as functions of covariates.

However, the age-specific breeding proportions can be estimated directly by fitting a JS model using the new parameterization defined in the previous section. Prior parameterizations of the JS model made this difficult because the total recruitment between sampling occasions was modeled, and it was impossible to constrain these to be non-negative or to simultaneously model several cohorts with common recapture, survival, or recruitment parameters. The new parameterization avoids many of the model fitting complications of Clobert et al. (1994) and lends itself to direct model selection and testing. Furthermore, the Schwarz and Arnason (1996) formulation also naturally leads to multiple-cohort settings. Refer to Clobert et al. (1994) and Schwarz and Arnason (2000) for the assumptions made in addition to those commonly made in CJS models.

In this new method, the mark applied at age 0 is used only to age the animals at subsequent recaptures; the first recapture is treated as an initial mark, and second and subsequent recaptures treated as recaptures after the initial mark. In this way, the population of animals who are breeders is treated as an open population in the JS framework. Animals that commence breeding are treated as new entrants into the population. By parameterizing births in the JS model by the proportion of the total entrants over the course of the study, these now correspond directly to the age-specific breeding proportions of interest.

Figure 1 illustrates the parameters as they would apply in a study with 2 cohorts of animals marked as young (for simplicity at age 0). Animals start to breed at age 1. Full breeding takes place by age 6. Recaptures take place one year apart over a span of 7 years. Observations on breeders start in calendar year 1, the first year when the first cohort starts to breed.

The most general model shown in Figure 1 is not very useful as each

cohort has its own set of parameters, and there is confounding of parameters at the start and end of the study (Schwarz et al., 1993). This implies that the age-specific probabilities are not estimable unless further assumptions are made. For example, the study could be extended at least one further occasion after the last age of breeding to ensure that $b_{g,T-i} = 0$ for all cohorts.

Resolving the confounding at the start of the study can be done by assuming that certain parameters are equal across cohorts or by modeling the capture probabilities as functions of covariates. For example, one may be willing to assume that $p_{1i} = p_{2i} = \dots = p_{Gi}$. Or, the $\{p_{gi}\}$ could be modeled as functions of covariates, as was done in Clobert et al. 1994, or possibly it may be tenable to consider models where $p_{gi} = p_g$ for all i .

Alternatively, it is sometimes possible to have a separate cohort of known breeders that were marked prior to the start of the first recaptures of the new breeders. In this case, this additional cohort could be used to estimate the p_{gi} (under the assumption of independence of recapture probabilities among cohorts).

Once the confounding problem has been resolved, the JS model can be fitted using the methods outlined in Schwarz and Arnason (1996) using the computer package *POPAN* (Arnason, Schwarz, and Boyer 1998).

Reduced models can also be investigated using likelihood ratio tests or AIC in the usual fashion. An interesting set of models is where the age-specific breeding proportions are stationary over time so that $b_{1i} = b_{2i} = \dots = b_{Gi}$.

Schwarz and Arnason (2000), and Schwarz and Stobo (2000) present examples of the application of this model to black-headed gulls (Clobert et al., 1994) and to grey seals.

The results of the model fitting procedures applied to the gull data are shown in Table 2. Here all breeding proportion estimates are non-negative (unlike in Clobert et al. 1994), and it is relatively easy to fit and test if a model with equal breeding proportions over cohorts is tenable.

The average age of first breeding is found directly and its standard error can be estimated from a Taylor-series expansion. By making further assumptions about the survival rate of non-breeders, it was also possible to estimate the juvenile survival rate. However, unless the cohorts were tagged as young, this would generally not be possible.

The JS method has a number of advantages over that used by Clobert et al. (1994):

- Estimates of age-specific breeding proportions are a fundamental parameter of the model and are easily estimated using the methodology of Schwarz and Arnason (1996).
- It is easy to constrain the estimates to be within the admissible range of 0-1 and to model them as functions of covariates.
- It is straight forward to examine models where the breeding proportions are equal among cohorts.
- The confounding among the breeding proportions, capture probabilities, and survival rates at the beginning and end of the study are now readily apparent and the modeler is aware of the need to estimate some of the confounded parameters to ‘free up’ the estimates of the breeding proportions.

Pradel (1996), Pradel et al. (1997), and Pradel and Lebreton (1999) used a different method based on a CJS model applied to the histories read backwards, to estimate the age-specific breeding proportions. These are computed based on the seniority probabilities as:

$$\beta_{i,Pradel} = (1 - \gamma_{i+1})\gamma_{i+2} \cdots \gamma_T$$

and are also shown in Table 2. Schwarz and Arnason (2000) showed that Pradel’s age specific breeding proportions are conditional upon animals surviving until the age at which all animals have become breeders. For long lived animals, his estimates of the age-specific breeding proportions should be very similar to the JS estimates. However, for short lived animals, his method will tend to overestimate the proportion in the older age classes, and underestimate the proportion in the younger age classes. This will lead to a positive bias in the estimate of the average age of initiation of breeding as seen in Table 2. Note that this approach, like ours, conditions upon the set of animals ever seen as breeders and also ‘ignores’ the marking occasion at age 0, which is used only to age the animals when recaptured.

As the age-specific breeding estimates are based on the proportion of new entrants, they should also be free of the biases induced by heterogeneity in capture probabilities.

5 Population Growth

The JS model was originally developed to estimate raw abundances. However, in many cases, this is of secondary importance and trend in abundance (population growth or decline) is of more ecological interest.

Nichols et al. (1986), Pradel (1996) and Pradel et al. (1997) used the CJS model to capture-histories read ‘backwards’ to estimate seniority probabilities (and subsequent fecundity) and population growth. However, as modeling histories in a forward direction leads only to estimates of catchability and survival, modeling histories in a backwards fashion leads to estimates of catchability and seniority. Consequently, it seems sensible to use a JS model to estimate all quantities simultaneously.

In the short term, population growth can be expressed in terms of the JS parameters (dropping the subscript g for convenience and ignoring losses on captures and injections) as:

$$\lambda_i = \frac{N_{i+1}^-}{N_i^+} = \frac{N_i^+ \phi_i + B_i}{N_i^+} = \phi_i + \frac{B_i}{N_i^+} = \phi_i + \frac{\beta_i}{(\beta_0 \phi_1 \phi_2 \cdots \phi_{i-1} + \beta_1 \phi_2 \phi_3 \cdots \phi_{i-1} + \cdots + \beta_{i-1})}.$$

Similarly, Pradel’s (1996) seniority probability can be expressed as:

$$\gamma_{i+1} = \frac{N_i^+ \phi_i}{N_{i+1}^-} = \frac{N_{i+1}^- - B_i}{N_{i+1}^-} = 1 - \frac{B_i}{N_{i+1}^-} = 1 - \frac{\beta_i}{(\beta_0 \phi_1 \phi_2 \cdots \phi_i + \beta_1 \phi_2 \phi_3 \cdots \phi_i + \cdots + \beta_i)},$$

which is simply the inverse of Jolly’s (1965) dilution rate parameter. Fecundity can be expressed as:

$$f_i = \frac{B_i}{N_i^+} = \lambda_i - \phi_i = \phi_i \left(\frac{1}{\gamma_{i+1}} - 1 \right) = \frac{\beta_i}{(\beta_0 \phi_1 \phi_2 \cdots \phi_{i-1} + \beta_1 \phi_2 \phi_3 \cdots \phi_{i-1} + \cdots + \beta_{i-1})},$$

which is the net births in the interval per member initially alive at the start of the interval.

Note that Pradel (1996, Section 6) defined fecundity as

$$f_{i,Pradel} = \frac{1}{\gamma_i} - 1 = \frac{B_i}{N_i^+ \phi_i} = \frac{f_i}{\phi_i}$$

which is the net births in the interval per member alive at the end of the interval.

As in the full JS model, some confounding of parameters may occur. For example, as in Pradel (1996), only λ_i for $i = 2, \dots, k - 2$ can be estimated as β_0 and β_1 are confounded with p_1 , and β_{k-1} is confounded with p_k . However, from Table 2 of Schwarz et al. (1993), the confounding structure is such that even though λ_1 cannot be estimated, $\lambda_2, \lambda_3, \dots$ can be estimated.

In all three cases, the estimates are obtained by simple substitution and the variances of the estimators can be obtained by a Taylor-series expansion. These estimates are presented for the capsid data of Jolly (1965) used by Pradel (1996) in Table 3a.

There are several advantages to considering estimates as function of the fundamental parameters rather than as intrinsic parameters in a new likelihood as done in Pradel (1996).

First, it clearly shows that these parameters are dependent both upon survival rates and new entrants. In Pradel (1996) formulation, both λ and ϕ appear as separate parameters in the likelihood which ‘overlap’ in their effects. The JS framework completely separates the effects of recruitment and survival which avoids numerical difficulties in model fitting. In addition, some care must be taken with the Pradel formulation in specifying models that are biologically appropriate. For example, it can be questioned whether it is sensible to fit models whose survival rates are different among groups, but the population growth rate are equal (which include a survival component). However, such compensatory mortality and reproduction models might be appropriate in certain cases. Two examples are: (1) where the two populations are ‘sinks’ with growth limited by external factors (e.g. total available habitat) and new entrants arriving from outside; and (2) where low survival is coupled with high reproductive output and high survival is coupled with low reproductive output (r-K tradeoffs).

Second, all estimates are automatically constrained to be consistent with each other. For example, $\hat{\lambda}_i$ can never fall below the estimated survival rate, $\hat{\gamma}_i \leq 1$, and \hat{f}_i must be positive. Pradel (1996, Table 3b) has estimates that violate these constraints but our results in Table 3a are consistent.

Third, Pradel also found that the maximum likelihood differed depending upon which parameterization was adopted leading to different estimates. This cannot happen in the JS framework where a single unique maximum likelihood is always found (Schwarz and Arnason, 1996).

The major difficulty in using the JS approach is fitting models where the derived parameters are equal across time or groups. Because these are non-linear functions of the fundamental parameters, techniques such as the design matrices used by *MARK* will not work. However, as shown by Schwarz and Arnason (1996), arbitrary linear or non-linear constraints can be imposed using the methods of Lagrange multipliers. An example of these constraints is shown in Table 3b. [Note that this reduced model is clearly not tenable and is only used to illustrate that such models can be fit.]

As noted in Section 3, heterogeneity in catchability can cause substantial bias in estimates of raw abundance or recruitment. Using a similar argument as in Section 3, the estimates of population growth, seniority, and fecundity should be relatively unaffected by heterogeneity. This has been confirmed by the author using the methods of Carothers (1973) and by simulations.

The long-term viability of a population is often investigated through the

use of Leslie matrices, where age-specific fecundity and survival rates determine the dominant eigenvalue of the population transition matrix. The JS approach provides a much more direct method - particularly if it is limited to the adult population. Note that ‘fecundity’ in the JS approach is not the same as ‘fecundity’ in the Leslie-matrix approach. In the JS approach, ‘fecundity’ is the net number of new adults produced per old adult. Hence this fecundity is a composite of the Leslie-matrix fecundities for the younger age classes plus the pre-adult survival. Furthermore, unless the population is in a steady-state age-distribution, there can be large changes in the JS ‘fecundity’ even if ‘real’ fecundity has not changed. As Pradel’s $\{\gamma\}$ are simple functions of the JS fecundity, they must also be interpreted carefully; hence models with a constant γ over time or among groups will only be reasonable in populations at an equilibrium age distribution. A referee noted that in fact the test of the hypothesis of a constant population growth rate could be used to test if the population has achieved a stable age distribution.

6 Future directions

The JS model has been the “orphaned child” of the triad of capture-recapture methods. This may have been driven by the old formulation of the likelihood which concentrated upon raw abundance estimates. However, as shown in the above sections, the JS model has a wider application than simply raw abundance estimation - it is important to think of any additions to a population as amenable to treatment in a JS framework.

Another drawback has been the lack of easy to use, comprehensive computer programs. However, *POPAN* (Arnason, Schwarz, and Boyer 1998) now includes all the features described above and work is underway to incorporate a version into the package *MARK*.

There are several areas of research that should be pursued.

The likelihood can easily be broken into three components. The components dealing with recaptures involved only the survival and capture rates while the recruitment component involved the recruitment, capture, and survival rates. Nevertheless, Schwarz and Arnason (1996) showed that in the full model (with no restrictions over time or groups), all of the information on the survival and capture rates is contained in the former component. I suspect that the majority of information on survival and capture remains in this component even under restricted models. Consequently, there should be little loss of efficiency in always using the former to estimate survival and catchability (i.e. do a CJS analysis), and then performing a conditional maximum likelihood analysis on the first component to estimate the recruit-

ment components. This would provide a relatively easy way to augment the *MARK* software package. A more systematic investigation is needed to verify this conjecture.

Second, if population growth is really the focus of the investigation, an alternate parameterization replacing the β_i 's by a term related to fecundity may be more appropriate. This would follow along the lines of Cormack's (1985, 1989) log-linear approach, but should be free of the problems in determining the estimated standard errors.

Third, standard Leslie-matrix models require age-specific fecundity and survival rates. The JS model can be easily modified to be age rather than time varying (Pollock 1981), but it treats all recruitment in the same fashion. It should be possible to modify the JS age model to estimate both age specific survival and age-specific fecundity if actual births could be identified or partitioned by cohort of origin. This would allow the parameters of a Leslie-matrix to be identified directly.

Fourth, as noted in Schwarz and Arnason (1996), the age-structured JS model could be reformulated along the lines of Schwarz and Arnason (1996). This may provide a method of distinguishing immigration from true births in much the same way as done in robust design (Nichols and Pollock, 1990; Pollock et al. 1993).

Finally, the robust design (Pollock 1982) is a hybrid design that combines features of both open and closed populations. It also allows the experimenter to investigate temporary emigration (Schwarz and Stobo, 1997; Kendall et al., 1997) in addition to survival and abundance. Additional work is needed to investigate if the recent revision to the JS model can be incorporated in the robust design, e.g. can the age-specific breeding proportions model be augmented by information on temporary absences from the breeding colony to estimate both the age-specific breeding proportions and the overall pregnancy success rate.

7 Acknowledgments

This work was supported by a Natural Science and Engineering Research Council of Canada (NSERC) Research Grant.

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Table 1: Estimates from model $\{p_g, \phi_t, \beta_{g*t}\}$ for salmon returning to spawn

Week	\hat{p}_i	$se(\hat{p}_i)$	$\hat{\phi}_i$	$se(\hat{\phi}_i)$	$\hat{\beta}_i$	$se(\hat{\beta}_i)$	\hat{B}_i	$se(\hat{B}_i B_i)$
Adult Estimates								
0					0.422	0.038	253.3	29.0
1.5	0.323	0.031	0.472	0.052	0.000	0.000	0.0	0.0
3	0.323	0.031	0.927	0.116	0.343	0.048	206.1	29.3
4	0.323	0.031	0.785	0.094	0.070	0.051	42.2	29.5
5	0.323	0.031	0.748	0.078	0.000	0.000	0.0	0.0
6	0.323	0.031	0.623	0.096	0.055	0.027	33.0	15.3
7	0.323	0.031	0.308	0.081	0.110	0.024	66.1	13.1
8.5	0.323	0.031	0.614	0.136	0.000	0.000	0.0	0.0
10	0.323	0.031						
Jack Estimates								
0					0.681	0.064	388.9	70.3
1.5	0.158	0.025	0.472	0.052	0.000	0.000	0.0	0.0
3	0.158	0.025	0.927	0.116	0.231	0.077	132.1	44.8
4	0.158	0.025	0.785	0.094	0.052	0.074	29.6	41.7
5	0.158	0.025	0.748	0.078	0.000	0.000	0.0	0.0
6	0.158	0.025	0.623	0.096	0.000	0.000	0.0	0.0
7	0.158	0.025	0.308	0.081	0.036	0.023	20.6	12.7
8.5	0.158	0.025	0.614	0.136	0.000	0.000	0.0	0.0
10	0.158	0.025						

Table 2: Estimates of age-specific breeding proportions from fitting two models with capture-probabilities a linear function of the number of visits (given in Table 4 of Clobert et al., 1994), breeding restricted to ages 2-5, and survival is constant over time and among cohorts.

Age	Each cohort allowed its own breeding proportions						Common breeding proportions for all cohorts		Common breeding proportions using Pradel's γ	
	Cohort 1		Cohort 2		Cohort 3		<i>Est</i>	<i>se</i>	<i>Est</i>	<i>se</i>
	<i>Est</i>	<i>se^c</i>	<i>Est</i>	<i>se^c</i>	<i>Est</i>	<i>se^c</i>				
2	.240	.169	.000	-	.401	.181	.299	.124	.214	.113
3	.339	.219	.553	.249	.214	.201	.356	.173	.316	.165
4	.000	-	.293	.314	.000	-	.001	.161	.001	.177
5	.422	.179	.155	.269	.385	.151	.344	.120	.470	.162
Average	3.604	.426	3.602	.413	3.370	.393	3.390	.296	3.727	.378
$\hat{\phi}^a$.808	.064	.808	.064	.808	.064	.806	.064	.806	.064
$\hat{\phi}_0^b$.076	.024	.109	.035	.094	.027	.091	.024		
log-likelihood			-185.1				-187.2			

^a Survival probability for breeders

^b Survival probability from the time of marking at age 0 to the first age of breeding.

^c Standard errors are not available when estimates of age-specific breeding proportions fall on the boundary of the parameter space - refer to Schwarz and Arnason (1996) for details.

Table 3: (a) Population growth and seniority estimates for Jolly's (1965) capsid data for an unconstrained model.

<i>i</i>	\hat{p}_i	<i>se</i>	$\hat{\phi}_i$	<i>se</i>	\hat{N}_i	<i>se</i>	$\hat{\gamma}_i$	<i>se</i>	$\hat{\lambda}_i$	<i>se</i>
1	1.00	-	0.65	0.108	n.e.	-			n.e.	-
2	0.28	0.085	1.00	0.000	513.9	150.7	n.e.	-	1.50	0.47
3	0.22	0.033	0.87	0.095	768.3	103.2	0.67	0.206	1.26	0.25
4	0.22	0.034	0.56	0.063	962.9	142.8	0.69	0.116	0.99	0.20
5	0.23	0.033	0.84	0.075	945.3	124.9	0.57	0.090	0.94	0.16
6	0.24	0.029	0.79	0.071	882.1	97.9	0.89	0.122	0.91	0.13
7	0.31	0.033	0.65	0.057	802.5	76.0	0.87	0.089	0.81	0.09
8	0.27	0.025	0.99	0.096	643.0	47.9	0.80	0.064	0.99	0.10
9	0.27	0.031	0.69	0.081	633.6	62.3	1.00	-	0.76	0.11
10	0.27	0.034	0.88	0.121	478.4	53.1	0.91	0.065	1.06	0.18
11	0.24	0.036	0.77	0.129	506.4	67.0	0.83	0.071	0.92	0.18
12	0.26	0.043	n.e.	-	462.8	70.8	0.84	0.078	n.e.	-
13	1.00	-			n.e.	-	0.95	0.080		

$\log - \text{likelihood} = -3117.1$

n.e. = not estimable

Table 3: (b) Population growth and seniority estimates for Jolly's (1965) capsid data under a constant population growth and capture probability model.

i	\hat{p}_i	se	$\hat{\phi}_i$	se	\hat{N}_i	se	$\hat{\gamma}_i$	se	$\hat{\lambda}_i$	se
1	0.25	0.010	0.57	0.067	659.7	37.3			0.998	0.007
2	0.25	0.010	0.90	0.080	658.3	34.2	0.57	0.067	0.998	0.007
3	0.25	0.010	0.71	0.067	653.8	31.5	0.90	0.081	0.998	0.007
4	0.25	0.010	0.54	0.053	647.3	29.2	0.71	0.068	0.998	0.007
5	0.25	0.010	0.81	0.065	638.9	27.4	0.54	0.054	0.998	0.007
6	0.25	0.010	0.81	0.062	631.5	26.4	0.81	0.065	0.998	0.007
7	0.25	0.010	0.69	0.048	628.1	26.1	0.81	0.062	0.998	0.007
8	0.25	0.010	1.00	0.007	619.7	26.4	0.69	0.048	0.998	0.007
9	0.25	0.010	0.78	0.050	617.4	27.5	1.00	-	0.998	0.007
10	0.25	0.010	0.88	0.062	613.0	29.1	0.79	0.050	0.998	0.007
11	0.25	0.010	0.86	0.056	610.6	31.2	0.89	0.062	0.998	0.007
12	0.25	0.010	1.00	0.007	606.3	33.6	0.86	0.056	0.998	0.007
13	0.25	0.010			604.9	36.4	1.00	-		

$\log - likelihood = -3236.4$

Figure 1: Relationship of parameters to sampling occasions in estimating age-specific breeding proportions

Cohort	Year						
	1	2	3	4	5	6	7
1	$\xrightarrow{b_{10}}$	$\xrightarrow{b_{11}}$	$\xrightarrow{b_{12}}$	$\xrightarrow{b_{13}}$	$\xrightarrow{b_{14}}$	$\xrightarrow{b_{15}}$	$\xrightarrow{0}$
		$\xrightarrow{\phi_{11}}$	$\xrightarrow{\phi_{12}}$	$\xrightarrow{\phi_{13}}$	$\xrightarrow{\phi_{14}}$	$\xrightarrow{\phi_{15}}$	$\xrightarrow{\phi_{16}}$
	p_{11}	p_{12}	p_{13}	p_{14}	p_{15}	p_{16}	p_{17}
2		$\xrightarrow{b_{20}}$	$\xrightarrow{b_{21}}$	$\xrightarrow{b_{22}}$	$\xrightarrow{b_{23}}$	$\xrightarrow{b_{24}}$	$\xrightarrow{b_{25}}$
			$\xrightarrow{\phi_{22}}$	$\xrightarrow{\phi_{23}}$	$\xrightarrow{\phi_{24}}$	$\xrightarrow{\phi_{25}}$	$\xrightarrow{\phi_{26}}$
		p_{22}	p_{23}	p_{24}	p_{25}	p_{26}	p_{27}

This is a two cohort study. Animals in cohort 1 start to breed at age 1; those from cohort 2 also start to breed at age 1 which is in calendar year 2. Animals are fully recruited to breeding status by age 6. The parameters b_{gi} measure the age-specific breeding proportion for cohort g at age $i + 1$. The parameters p_{gi} are the year specific capture probabilities for cohort g in year i . The parameters ϕ_{gi} are the probability of survival from year i to year $i + 1$ for animals in cohort g . The $\xrightarrow{\quad}$ indicates that the parameter refers to the interval between capture occasions.