Review of stage-frequency data analysis methods

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ABSTRACT

Surveying number entering a particular stage of a stage-structured population (e.g. arthropods) using field sampling data has been subject of many studies in last 60 years. Stage-frequency data consist of count of individuals in different development stages in samples taken from a population over a period of time. Several methods are then available for deriving estimates of stage-specific survival rates and other population parameters that are of interest to the ecologists that Manly (1990) listed 23 methods. The application of some of these methods is limited by their computational difficulty and others are limited by restrictive assumption that they make. Each method has advantages and disadvantages which arise from its assumptions. The first method in this field may be offered by Richards and Waloff (1954). Richards *et al* (1961), Dempster (1961), and Southwood and Jepson(1962) suggested further methods and the KNM method proposed by Kiritani & Nakasuji (1967) and extended by Manly (1974). There is therefore something of a problem for the data analyst to decide what is the best for a particular set of data. The purpose of this note is presenting a review of some important and applicable methods to show differences among these. So, it is recommend that any method be used with respect to the required information and parameters.

Introduction

Surveying number entering a particular stage of a stage-structured population using field sampling data has been subject of many studies in last 60 years and it is a basic step in the construction of life budgets. If a population containing individuals developing through several stages regularly be sampled over whole generation, then it is possible to estimate the number of individuals entering successive stages. Stage-frequency data consist of count of individuals in different developmental stages in samples taken from a population over a period of time. There are various methods invented for collecting required information to construct a life budget from stage-frequency data that Manly (1990, Table 4.2) lists 23 methods, and others probably also exist. There is therefore something of a problem for the data analyst to decide what is best for a particular set of data. The application of some of these methods is limited by their computational difficulty (Ruesink, 1975; Ashford, *et al*, 1970; Bierly, 1977) and others are limited by restrictive assumption that they make. The differences between these methods lies in the assumptions and number of parameters estimated. The common point of all these methods is estimation of number of individuals which enter successive life stages as well as stage survival rate. Each method has advantages and disadvantages which arise from its assumptions. These assumptions cause bias and computational limits with respect to real data.

Stage-frequency data consist of count of individuals in different development stages in samples taken from a population over a period of time. Such data are usually are collected in order to estimate the mean duration of stages, stage-specific survival rates, unit time survival rates, and total numbers entering different stages. These data in calculation of the total number of insects entering a stage and total stage mortality are used that these are base for key factor analysis. The first step in the construction of models for an insect population is often the

analysis of stage-frequency data for building stage specific life tables. Consequently, it is important for the biologist to have a range of straightforward and reliable methods for estimating population parameters from stage-frequency data. Some or all of the following parameters are likely of interest for a researcher to estimate: total number of individuals entering each stage, the average time spent in each stage, the probabilities of surviving each stage or the stage-specific survival rates, the mean time of entry to stages and unit time survival rate.

Stage-frequency data analysis methods

One of the first methods in this field is Richards and Waloff's (1954) method. This method is based on calculation of the slope of line that is the best estimator of the population decline after peak. By taking the cumulative number of stages ending to the concerned stage in logarithmic scale, the mentioned straight line, will exterpolate backward up to the beginning of the generation to obtain initial number of the concerned stage. This method work well for populations, which develop rapidlyand have a well defined peak.

In Richards *et al* (1961) method all stage mortality and constant daily mortality rate can be estimated if the initial number of the population, under curve area, and the duration of the instars be known.

Dempster (1961) described a method which has certain advantages over the earlier methods. Primarily it does not require one beware from the duration of each instar and the initial number of the first stage. Secondly, this method is independent of the rate of build-up of the population, although this rate must be known. This analysis is applicable to insects with distinct generations, that is a particular stage in one generation does not overlap the same stage of the next one.

The Southwood and Jepson's graphical method (1962) is a simple and still applicable method in realistic situations in which the daily survival rate varies from stage to stage, or when a full set of data is not available for the entire generation. This method

needs one beware of stage duration and the majority of mortality occurs at the end of a stage. Violation of the recent assumption leads to bias in estimations of this method. Some studies have been focused on improvement of the method assuming more real patterns of mortality distribution (e.g. Sawyer & Haynes, 1984). Sawyer and Haynes method is a correction of Southwood and Jepson method by including a constant daily rate of stage mortality.

Kiritani and Nakasuji (1967) first described their method for estimating stage specific survival rates of a population developing through several life stages that it had a restriction as requiring a fixed sampling intervals and did not estimateanyt parameter other than stage-specific survival rates. Manly (1976, 1977, 1985) overcame these two limitations.

Kobayashi (1968) assumed that the number entering the first stage is known, and then in a two-step procedure calculated and corrected sequential stages' mortality. He calculated stage mortality by shared consecutive reductions after peak between stages according to frequency of every stage in each sample (which indicates density-dependent stage mortality and in some cases is a logical assumption). Then according to the time-frequency distribution of each stage, he corrected it and assumed mortality during each stage is constant but differs among stages. He counted all reduction after peak as a mortality.

Read and Ashford (1968) and Ashford *et al* (1970) proposed the first statistical model with using a maximum likelihood method that estimates number of individuals entering each stage, daily survival rate and stage duration. After them, Rigler & Cooley (1974), estimated number of individuals entering each stage and stages duration, but many arguments did carry out against this method by Hariston & Twombly (1985), Aksens & Hoisaester (1987), Hariston *et al* (1987), and Saunders & Lewis (1987). In the same year, Lakhani and Service (1974) estimated all stages' survival rate by calculating under curve area of the stage-frequency data assuming stage durations and survival rates are known up to the last stage.

In Ruesink (1975) method we can calculate stage specific survival rates that vary with time providing the duration of each stage be known. Bellows (1977) and Bellows & Birley (1981) estimated both number of insects entering successive stages and stage survival rates using linear regression method by number of individuals entering the first stage being known. Derr & Ord (1979) calculated stage-specific survival rates when stages duration was known. Survival function in Kempton (1979) method did not depend on the stage. Kempton could calculate duration mean and number of individuals entering a stage if stage duration or alternatively proportion of two successive stage durations be known. Bellows *et al* (1982) estimated survival rate by stage-frequency regressed on time and other parameters estimated by Bellows & Birley (1981) method. Thus, they could calculate survival rates varying with time, stage duration and number entering each stage.

van Straalen (1985, 1982), assuming that each individual has a specific but measurable development time that vary according to a growth function, calculated number of individuals entering each stage, survival time, and duration of each stage, by maximum likelihood method in which physiological time was used instead chronological time to take the environment temperature effect into account.

Osawa et al (1983), Stedinger et al (1985),Dennis et al (1986), Kempton & Besag (1986), and Munholland et al (1989) assumed that growth has a normal or logistic function and temperature effect was included as physiological time and thus

population ratio was estimated at different times and stages by maximum likelihood method.

Bellows and Birley (1981) invented a method that had advantages over other methods. This method does not assume constant mortality rate in all stages and do not need to investigate all stages but only need to consider the first stage and the next one and also mortality rate in each stage.

Manly (1990) noted that most stage-frequency data models are deterministic However, a number of stochastic models such as Kempton method is found among them.

Mathematical models
Southwood & Jepson graphical method (1962)

Southwood & Jepson method is one of the easiest methods that be done with a minimum calculation. This method is applicable when some generation data is not

complete and when daily survival rate is different in various stages. This method does not require any assumption about the timing or distribution or sampling in equal intervals. Therefore, it is the most widely used method. In this method, it is assumed that all death occurs at the end of a stage and also need stage duration be known .

Pedigo and Zeiss (1996) have noted that the time scale for immature stages is degree-day and for mature stages sampling dates are used. Bellows *et al* (1989) developed this method by entering constant mortality into model. The general equation is as follows:

$$A = \int_0^T n_r(y)dy \int_0^D g'(x)dx$$

In which *A* is area under the curve, and the first integral represents number of entering to the stage and the second integral represents mortality.

This method is sensitive to high stage mortality that causes noticeable bias. Unfortunately, this bias determined only by direct measurement of recruitment rate of each stageand there is no simple method for estimating it.

Richards and waloff (1954)

This method has two basic assumptions. One of them is a distinct peak for each stage and the other one is the same mortality rate during all stages. Thus, recruitment takes place in a pulse. In such a case, the number of individuals at any stage of time t is:

$$Y_t = N_0 \emptyset^t$$

In which N_0 is the number of individuals at peak and $\emptyset$ is daily survival rate. If two regression lines be obtained before and after migration, the difference between estimated Yt for the two lines, represents rate of the migration (waloff and Bakker, 1963).

Manly (1974)

In this method the duration of stages, the number of insects entering the first stage and the rate of entry to stage do not have to be known but can be estimated and finally samples do not have to be taken at regular intervals. The method is somewhat similar to that of Richards and waloff but the time of entry to stages is assumed to follow a normal distribution and this means that there is no need for stages to show distinct peak in numbers.

Suppose that the time that insects enter a stage follows a distribution with frequency function $f(x)$. Suppose also that the survival rate per day after entry to the stage is $e^{-\theta}$, so that $\emptyset$ denotes the age specific death rate.

Then the probability that an insect enters a stage at time x and is still alive at time t is $e^{-\theta(t-x)}$. Hence the expected number of insects in the stage at time t is given by

$$Y_t = N_0 \int_{-\infty}^{t} e^{-\theta(t-x)} f(x)dx \text{ ,}$$

Where N_0 is the total number of insects entering the stage. And f (x) at time of x is the distribution of stage frequency.

Ruesink (1975)

This method provides separate estimates of survival rates for each stage. The basic equation is:

$$\emptyset_{j,j+1} = \frac{C_{j+1,t+n} - C_{j+1,t-n}}{D_{j,t+n} - D_{j,t-n}}$$

In which ∅ is survival between stages j and j+1,Cj+1 is total number of individuals entering stage j+1 between time t - n to t + n and, similarly, Dj is the number of individuals leaving stage j in the same interval that both of them estimate using Richards and Waloff'd (1954) method. The n is an optional value that choose larger when sampling error is high.

Dempster (1961)

This method requires a separate estimate of the first stage's recruitment and all stages should be sampled two time more than number of stages. Assuming a constant mortality (μ):

$$Y_t - Y_0 = N\alpha(0 \to t) - \frac{(I_0 + I_t)}{2} t\mu_1 - \frac{(II_0 - II_t)}{2} t\mu_2 \cdots \cdots - \frac{(A_0 + A_t)}{2} t\mu_\alpha$$

Y_0 and Yt in this equation is the total population at time 0 and t, N the total number of first stage that obtained independently. α (0→ t) is ratio of the hatching occurs between times 0 and t, and the remaining sentences are average of number of individuals in each stage from stage one (I) to adult (A). The μ values are unknowns that must be estimated regard to sampling data. Additionally, the multiple regression can be used to estimate the unknown values. This method can also include migration (southwood and Henderson, 2000).

Richards and waloff's second method

This method proposed By Richards *et al* (1961), but Southwood and Henderson (2000) called it second method of Richards and waloff. This method is used when recruitment and mortality have considerable overlap. This method needs the independent estimation of the first stage (usually eggs) and the duration of each step in laboratory. The basic equation is:

$$N_i = n \int_0^a k^a dt = \frac{n(k^a - 1)}{\ln k}$$

N_i is number of individuals that counted at each sampling date, n is the number of stages and a is stage duration. The only unknown factor in this equation is k or the survival rate that by solving the equation for k, amount of the next stage n is estimated. Mortality rates can be derived from equation 100 (1-k^a). The same calculations continue to the final stage. These estimates are very sensitive to the error of a. A minor error about half of the time unit, can cause large errors in estimating n and k.

Kiritani, Nakasuj, Manly method (KNM)

This method was originally developed by Kiritani and Nakasuji (1967) and Manly (1985, 1977, and 1976) modified it for entering sampling with unequal intervals into calculation and estimating more parameters. To use this method, three conditions are necessary, the constant survival rate for the entire growth period, no migration and a sampling that include all generation that begins before entering the first stage and finishes after terminating the last stage. If the later requirement does not meet, iterative KNM method may used for estimating population parameters (Manly, 1990; Young and Young, 1998).

This method consists of the following procesures:1. calculating the under curve areas of the stage-frequency and time-stage frequency data using the trapezoidal rule and 2. estimating the basic parameters of the population. The basic equation is:

$$f_i(t) = M_j \int_{t-a_j}^{t} g_j(x) e^{-\theta(t-x)} dx$$

The concept of this equation is that the frequency of individuals in stage j at time t is the number entered in time t-aj and survived to time t . The $g_j(x)$ function is the density function, $e^{-\theta(t-x)}$ is survival probability from time x to t, M_j is all individuals entering stage j and $f_i(t)$ is the stage frequency at time t.

Sawyer and Haynes method (1984)

Due to the advantages of the Southwood and Jepson graphical method Sawyer and Haynes tried to correct it. Southwood and Jepson's estimates of survival rate includes several sources of errors for example, bias aroused from systematic sampling techniques, the unequal efficiency of sampling techniques for different stages, sampling random errors, the error due to large sampling intervals, and the error caused by calculation of stage duration in the field, the first four errors are related to sampling techniques; Thus, they can control by increasing the sample size or improving sampling techniques. Sawyer and Haynes solved the fifth mentioned error, this error was related to Inaccurate estimates of life duration (T) in field.

Southwood and Jepson method underestimated the number of individuals entering a stage. Mean duration of life for the population with constant mortality, can be corrected easily by $\left[\frac{S-1}{\ln(S)}\right]$. Thus, the number of insect entering a stage with correction will be defined as follows:

$$N = A/\mu = A/[T(S - 1)/\ln(S)]$$

(N) is The number of individuals entering each stage, (T) is time period, (μ) is Stage mean and (S) is Survival of Stage.

Conclusions

Several methods are therefore available for deriving estimates of stage-specific survival rates and other population parameters that are of interest to the ecologists.

Complicated mathematical models of Read and Ashford (1968), Ashford *et al* (1970), Kempton (1979), and Van Straalen (1982 and 1985) have the ability to use survival rates in different stages or ages. In contrast, the methods of Richards *et al* (1961), Southwood and Jepson (1962), Lakhani and Service (1974), Mills (b1981), Dempster (1961), Kobayashi (1968), Berley (1977) and Bellows and Berley (1981) are relatively simple but require some independent data, including each stage duration number of entering first stage or entering time to the first stage.

Each of these different methods have their advantages and disadvantages, for instance, Richards and waloff's second method is used when recruitment and mortality have considerable overlap. This method needs independent estimate of the first stage (usually eggs) and the duration of each step in laboratory. These estimates are very sensitive to the error of stage duration (a).

Bellows and Birley method does not assume constant mortality rate in all stages and do not need to investigate all stages but only need to see the first stage and next stage of growth period and also mortality rates in each stage.

The Dempster method has shown less bias than any others method but the estimates from this method have been so variable that it must be rejected as unsatisfactory for normal use.

The Southwood and Jepson's graphical method is a simple and still applicable method in realistic situations in which the daily survival rate varies from stage to stage, or when a full set of data is not available for the entire generation. This method

needs one beware of stage duration and the majority of mortality occurs at the end of a stage. Violation of the recent assumption leads to bias in estimations of this method. Some studies have been focused on improvement of the method assuming more realistic patterns of mortality distribution such as Sawyer and Haynes method that it is a correction of Southwood and Jepson method by including a constant daily rate of stage mortality.

Therefore recommend that any of these methods be used with respect to the required information. For example, when no information is available about the number of insect entering the first stage, Sawyer and Haynes method is a suitable method. But when number of insect entering the first stage is known, the second Richards and Wallof method will be preferred.

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