

Use of individual-based models for population parameters estimation

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ABSTRACT

A method for parameters estimation of stage-specific mortality and fecundity rate functions in poikilotherm organisms, and in particular for arthropod structured population, is proposed. The application of this method requires three types of information: stage-frequency data of a sampled population, development rate function and time evolution of forcing variables affecting the rate functions. By means of an individual-based model (a microscopic model) the number of eggs produced by the adults is generated starting from the number of individuals collected at each sampling time. Using a compartmental model (a macroscopic model) a stage-structured population dynamics is described and compared with observations. Non-linear regression methods based on least square principle are used to estimate the optimal parameters of the mortality and fecundity rate functions combining microscopic and macroscopic models. As a case study, the parameter estimation of the temperature-dependent mortality function of olives fruit fly Bactrocera oleae is presented.

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1. Introduction

A critical point in modelling populations dynamics, and in particular for arthropods, is to have biodemographic functions, such as development, fecundity and mortality rate functions, with a solid biological background and known parameters (Carey, 1993, 2001). However, parameter estimation is one of the weak points in ecological modelling (Jørgensen, 1997; McCallum, 2000). If it is possible to set up laboratory experiments where population dynamics is led to the simplified situation of a single cohort life table, biodemographic functions as well as their parameters can be easily estimated (Manly, 1989). In some cases it is not possible to perform parameter estimation in laboratory or experimental data are not sufficiently reliable, in particular for fecundity and mortality functions. In such cases it is necessary to resort to the analysis of stagefrequency data coming from field population sampling.

Sophisticated demographic methods have been proposed to analyze stage-frequency data, they are thoroughly discussed by Manly (1989, 1990). However such methods display a series of important problems specially referring to the population of arthropods. In particular, three categories of problems can be recognized. (i) Technical problems may derive from the use of chronological time in life tables analysis, while the development of a cohort is better described by its dependence on physiological time (as a function of biological and environmental parameters). Therefore, the transformation of chronological time into physiological time can be necessary, even if complex in some cases, and stage-specific development rate functions and time series of temperature data are needed. (ii) Further problems concern sampling procedure and sampling variables definition. Sharp differences in stage biology (frequently due to high mobility of adults) may make hard or impossible the use of a single sampling technique for the

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different stages of a species and to convert different estimates in a common definition of density. The consequences of this limitation may be heavy, and equivalent, in practice, to the lack of information on adult abundance making impossible the fecundity estimation. (iii) The most important problems in the application of classical demographic approaches to the analysis of field stage-frequency data, arise when mortality and fecundity patterns are interested by complexity deriving from both species-specific life-history strategies or responses to variation in environmental forcing variables. In particular, in the analysis of life table mortality rates are assumed to be equal for all the individuals in the population or at least within a stage. In some cases this condition can be accepted, in many other cases this is not admitted mostly because of both natural or man made fast variations concerning environmental conditions (e.g. abrupt changes of temperature) or resources (e.g. variation in plant content and biomass which determine resource suitability, acceptability and availability for a phytophagous, see Schowalter, 2000). Concerning the fecundity, the analysis of stage-frequency data with recruitment is relatively simple under the hypothesis that the effect of reproduction occurs in the first stage for a short period of time. Such instantaneous generation of a new cohort does not hold in the case of continuous reproduction, given that the income in the first stage depends on the uninterrupted contribution of adults present in the population and on their physiological age distribution (Manly, 1989). In such cases many problems arise in parameter estimation, particularly because the intra-stage frequencies change also for the continuous appearance and development of new individuals.

Demographic patterns characterized by continuous recruitment with partially or completely overlapping generations are particularly important since this is the typical situation of iteroparity, a common reproductive strategy in arthropod species. In these conditions it is possible to analyze the life-table if at least one of these conditions holds true (Manly, 1989): (a) it is possible to link the recruitment in stage 1 to the number of individuals in the population; (b) the time distribution of the incoming organisms is sufficiently simple and it can be described with few parameters. This can be done only by demographic models. Most of them assumes that the age of the individuals is known, in this case two different approaches can be adopted: methods based on Lotka integral equation (Manly, 1989) and methods based on matrix models, like, for example, the Leslie matrix (Caswell and Twombly, 1989; Caswell, 2001). As an alternative to these approaches, whose main limits are in the assumptions they are based on, many other empirical methods have been proposed that reduce to the minimum the assumptions for the analysis. These methods start from stage-frequency data and refer to different types of population dynamics models. Among them are the approaches based on the compartmental model proposed by Elster (Faddy, 1989; Cappio Borlino et al., 1991; Di Cola et al., 1999) and those derived from the McKendrick-von Foerster model (Wood and Nisbet, 1991; Wood, 1994). Potentialities of these simulation methods are considerable since they allow estimating at the same time mortality and reproductive profiles as a function of time and/or age. However, even if they are able to deal with many unknown parameters,

they require a known functional form for both mortality and reproduction.

To overcome problems affecting classical demographic methods dealing with continuous recruitment and overlapping generations, a new modelling approach is here developed with the specific objective to estimate parameters in mortality and fecundity rate functions of given functional form in poikilotherm organisms and arthropods in particular. This method relies on the joint use of two simulation models: a microscopic or individual-based model, IBM (or i-state model) and a macroscopic or classical model (p-state model) (Metz and Diekmann, 1986; DeAngelis and Mooij, 2005). The microscopic model is a particle-based model (Hockney and Eastwood, 1989) which considers as inputs the stage-specific developmental rate functions of the species, the stage-frequency data collected at discrete time points, and the time evolution of forcing variables affecting development, mortality and fecundity. Starting from these information the IBM is able to define the individual age distribution and the profile of newly laid eggs (recruitment) along both the continuous chronological and physiological time, tackling the limit of classical demographic approach above described in point (i). The macroscopic model is a compartmental model (Di Cola et al., 1999) used to simulate the dynamics of a structured population where the recruitment is obtained via the microscopic model and the transferring functions are given by development functions. In the estimation procedure, through the application of nonlinear regression method based on least square principle the optimal parameters of the mortality and fecundity rate functions are obtained combining microscopic and macroscopic models.

Moreover, a special case where no information on adult abundance and/or development rate function is available is considered to address the problem (ii) that classical as well as modelling approaches encounter in such situations. In this case, by means of the individual-based model the profile of emerging adults along both chronological and physiological time is reconstructed. Then, under the assumption of known adult survival profile an estimate of the fecundity function can be derived. The special case is also able to tackle problems deriving from physiological age definition and measurement in the adult stage.

Since the method here proposed deals with poikilotherm organisms, the development is considered as temperaturedependent. As mentioned above, if temperature data series are available it is possible to overcome difficulties in describing life tables according to physiological age and time. Moreover, the approach here developed takes into account that especially in arthropods mortality and fecundity are influenced by external forcing variables, often by temperature. The method is able to define the dependence of mortality and fecundity rate functions from forcing variables which temporal dynamics is known, addressing the problems deriving from intra-stage variability in species-specific life-history strategies (see problem (iii) in the list above).

Noteworthy is the contribution offered by the individualbased model in the method here proposed, according to the importance assigned by many authors to such modelling approach in parameter estimation (Fahse et al., 1998; DeAngelis and Mooij, 2005). The main advantages we obtained Download English Version:

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