

Population Models - Size and Stage structure

When does size/stage matter?

Characterizing population dynamics can be done from an individual-perspective (i-state) in which we track individuals with different characteristics (age, stage, size, etc.) or can be done at population-perspective (p state) in which we characterize a population as having a density function (size or age distribution for example). Basic population models characterize a population by a single p-state variable (population abundance). Demography classically used age as an i-state variable, and characterized the population with the p-state variable of the age distribution. For many populations, this characterization is inadequate - when knowing the age of an individual doesn't provide a good basis for predicting its survival or reproduction. In this case, knowing the population distribution of age doesn't allow projection of population dynamics. Typical alternative i-state variables are size, stage (e.g. developmental stage such as instar), physiological state (e.g. lipid content), or location, or some combination of these.

When is age inadequate? This depends upon how much relevant information age provides about survival and reproduction of individuals. Caswell gives 3 main cases for which age alone is not sufficient:

(i) Size-dependent vital rates and growth very plastic. Here individuals of the same age can vary significantly in size, so age tells us little about an individual's size and reproduction. This is most readily apparent in species with large ranges of adult body size due to indeterminate growth. Examples include:

Species with a threshold size to reproduce (many perennial plants, crabs, fish)

Arthropods developing through discrete stages (instars) that must reach a certain stage before becoming reproductive.

Once reproduction begins, it may be allometrically related to body size (herbaceous plants, trees, kelp, molluscs, fish, amphibians, turtles)

Can be complex interaction between age, size, etc on reproduction - size dependence of sexual changes in fish (sequential hermaphroditism)

Size dependent mortality - modular organisms such as coral in which mortality decreases significantly with size (corals, herbaceous plants).

Note that size-based vital rates are not sufficient by themselves to rule out the use of age to characterize population demographics. If size is very well estimated by age, then use of age-structure would be adequate. It is growth plasticity which leads to individual variation in size as a function of age that limits the use of age alone.

(ii) Multiple modes of reproduction: many organisms have both sexual and vegetative reproduction, and if similar-aged offspring derived from each of these differ greatly in their survival and fertility, then age is an inadequate descriptor of demography.

(iii) Population subdivision and multistate demography: Here if a population is subdivided and the vital rates in the different subpopulations are strongly linked to local environmental factors, then an appropriate state variable would include age and the local environmental conditions. - multistate demography means that i-states are multidimensional.

Life Cycle graphs:

This is a graphical representation of the life stages and flow of individuals between them. Procedure is to:

- (a) Define a projection interval (this affects the structure of the graph)**
- (b) Define a node and number them for each life stage**
- (c) Put a directed line or arc from one node say n_1 to another say n_2 if there is some flow of individuals from n_1 to n_2 during a projection interval - that is if an individual in state i at time t can contribute individuals (by change in state itself or by reproduction) to state j , draw a directed arc from i to j .**
- (d) Assign each arc with a coefficient a_{ij} giving the per individual contribution of individuals from state i to state j in a time period. These coefficients can therefore be transition probabilities (e.g. the probability that an individual in state i grows into state j in one time period) or they can be reproductive outputs from state i individuals creating state j individuals.**

The projection matrix is then made up of these coefficients, and just as in the age-structured case, allows projection of structure changes in the population from one time to another. Unless there is some inherent periodicities in the life cycle of the organisms (e.g. bamboos which only reproduce very occasionally), projecting a population forward in time will lead to a stable stage distribution (similar to stable age distribution) after a long time. There are a number of relatively simple conditions to check for the projection matrix or the life cycle graph to ensure this occurs (*irreducibility*, meaning no subgroup of stages that is self contained such as a postreproductive class, and *primitivity* meaning that it is not cyclic). The rate of approach to the stable stage distribution depends upon the ratio of the dominant eigenvalue of the projection matrix to the magnitude of the first sub-dominant eigenvalue (the so called damping factor). For the vast majority of estimated life cycle graphs, the population would be projected to grow exponentially eventually with a stage distribution given by the dominant eigenvector and growth rate the dominant eigenvalue.

Sensitivity analysis:

This refers to investigating how the results of analysis of the projection matrix (such as the asymptotic growth rate and stage structure) would vary if the matrix were changed. This may be of interest to do for:

- (1) measuring how important a particular vital rate is to overall population growth - how much does a change in mortality or reproduction of one stage affect overall population growth?**
- (2) evaluating the effect of errors in estimating the vital rates on the population growth rate and stable stage distribution**
- (3) quantifying the effects of environmental perturbations which can modify the mortalities and fertilities in the projection matrix - life table response experiments**
- (4) evaluating alternative management strategies which lead to increases in mortality in some stages (say due to harvesting) but not in others.**
- (5) predicting the intensity of natural selection. This views the growth rate as a measure of fitness and investigates the effects of different genotypes with different stage dependent vital rates on population fitness.**

A sensitivity analysis typically involves determining the derivative of the dominant eigenvalue as a function of the elements of the projection matrix. There is a simple analytical form for these, determined just by knowing the left and right eigenvectors associated with the dominant eigenvalue (v = vector of reproductive values and w = vector of stable stage distribution) by

$$\mathbf{d}\lambda/\mathbf{d}a_{ij} = v_i w_j / (v, w)$$

where this is a partial derivative and the denominator on the right is the dot or inner product and λ is the dominant eigenvalue. To compare these though, they must be put on similar scales by normalizing them, giving the elasticities:

$$e_{ij} = (a_{ij} / \lambda) \mathbf{d}\lambda/\mathbf{d}a_{ij} = \mathbf{d} \log(\lambda) / \mathbf{d} \log(a_{ij})$$

which gives the proportional change in the population growth rate with

a proportional change in the vital parameter a_{ij} .

Time-varying models:

Here we view the projection matrices as time varying due to external environmental factors affecting the individual demographic parameters. These variations can be:

(a) deterministic - periodic environments, in which case the analysis isn't too complex as long as the focus is on the population at the period associated with the environmental periodicity.

(b) deterministic - aperiodic - here the sequence of environments does not repeat and therefore the demographic parameters do not either.

For both (a) and (b) there are a number of ergodic results under most circumstances - i.e. leading to long-term approach of the population structure to a stable stage distribution.

(c) stochastic environments with either time-homogeneous distribution (e.g. distribution of random environmental states does not vary with time) or non-time homogeneous distribution. The latter would occur for example in the global warming scenario.

(d) stochastic environments with or without some temporal correlation structure, so that successive environments are like independent coin tosses or not.

Again there are some ergodicity results here, which hold in some average sense - see Tuljapurkar's book.

Density dependent models:

Here the projection matrix depends either upon overall population density or upon the whole distribution of densities across stages. So linear analysis no longer applies and there can be a very complex set of behaviors of the projection model.