Stage, age and individual stochasticity in demography

Hal Caswell (2009)

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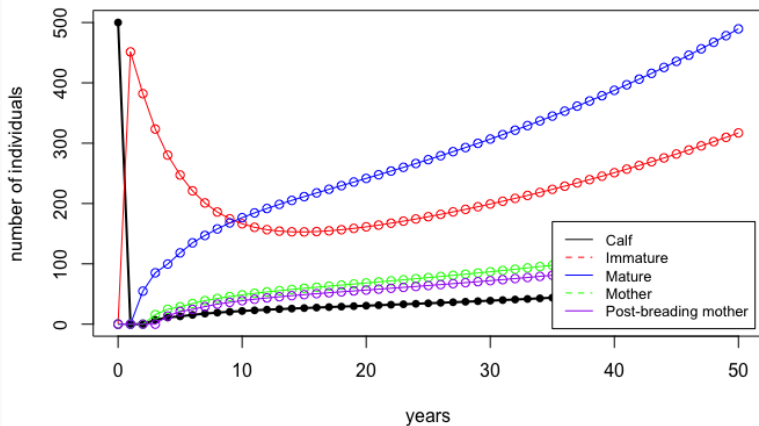
The North Atlantic right whale

North Atlantic right whales are among the most endangered whales on the planet. Once, thousands of right whales could be found in the Atlantic ocean, but by the late 1880s they had been hunted to near extinction. **Today, only about 500 remain.**
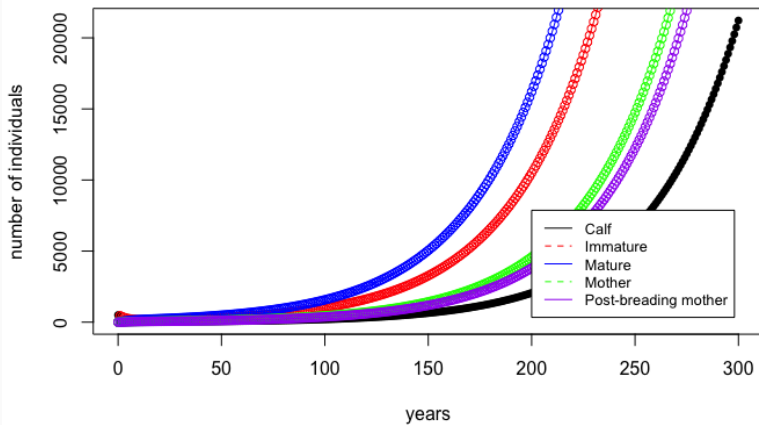
Background

Individual right whale can be photographically identified by scars and callosity patterns. The New England Aquarium has been surveying the population since 1980, accumulating a **database of over 10,000 sightings**.

The first year an individual is first identified is treated as "marking", the other times are marked as "recapture". This permits to use **mark-recapture statistics** and estimate the demographic parameters of this species.

Simulated NAW Population Growth

Simulated NAW Population Growth

Legend:
- Calf
- Immature
- Mature
- Mother
- Post-breading mother

(x-axis: years; y-axis: number of individuals)

Two modelling approaches

Age or stage-classified theories

One focus of demography is the study of the connection between the life course of individuals and the dynamics of the population.

Individuals differ along various dimensions:

1. age $\Rightarrow$ **age-classified theories**;
2. other characteristics (e.g. size, maturity etc.) $\Rightarrow$ **stage-classified theories**.

The two approaches are strictly related: even when the demographic model is entirely stage-classified, age is still implicitly present. Each individual becomes one unit of age older with the passage of one unit of time.

Individual stochasticity

Each life course can be thought as a process with **some individual stochasticity.**

Consider a newborn individual who grows through the different stages of life. In each stage, it is exposed to various mortality risks. Risks are often stochastic processes, and they might cause the lives of any two individuals to differ.

It follows that the **age-specific properties of an individual (e.g. longevity) can be modelled a random variable.** Then, we can look at the distribution of these properties among individuals and characterize their moments (i.e. mean, variance etc.).

Life cycle as Markov Chain

We start by thinking of the **life cycle as a Markov Chain** which ends with death (absorbing state).

In this setting, a Markov Chain models the **movement of an individual among a set of stages.** The probability distribution of the next stage of an individual does not depend on earlier states and may depend on the current state.

We can account for all the possible pathway and the relative probabilities that an individual can follow through life.
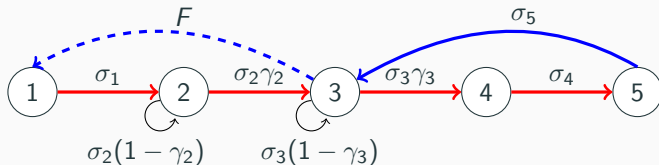
Stage-classified model

Stage-structured matrix population model
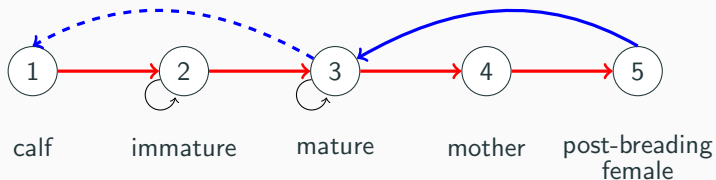
Projection interval is one year

Stage-structured matrix population model

Legend:

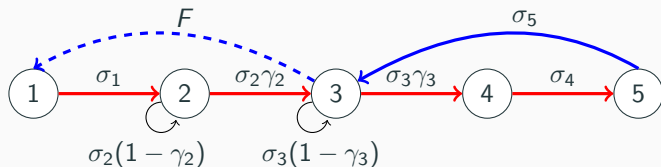stage $1 =$ calf

stage $2 =$ immature

stage $3 =$ mature

stage $4 =$ mother

stage $5 =$ post-breading mother

$\sigma_i =$ survival probability from stage i to $i+1$

$F =$ fertility

Stage-structured matrix population model

$$A = \begin{bmatrix} 0 & 0 & F & 0 & 0 \\ \sigma_1 & \sigma_2(1-\gamma_2) & 0 & 0 & 0 \\ 0 & \sigma_2\gamma_2 & \sigma_3(1-\gamma_3) & 0 & \sigma_5 \\ 0 & 0 & \sigma_3\gamma_3 & 0 & 0 \\ 0 & 0 & 0 & \sigma_4 & 0 \end{bmatrix}$$

Stage-structured matrix population model

a_{ij} is the (i,j) entry of the matrix **A** and represents how many individuals that will be in stage i in $t+1$ are produced by an individual who is in stage j in t (i.e. the per capita production).

This production may occur:

1. by the transition of an individual from stage j to stage i;
2. by the production of one or more new individuals (e.g. by reproduction).

Stage-structured matrix population model

We can interpret the matrix **A** as:

$$\mathbf{A} = \mathbf{U} + \mathbf{F} \tag{1}$$

where **U** is a matrix describing transition probabilities of extant individuals and **F** is a matrix describing the production of new individuals.

Note that the column sums of U are all less than or equal to 1 because the stages contained in U are transient states and mortality probabilities are not included.

Estimated transition matrix for the right wale

U and **F** are estimated by applying multi-stage mark-recapture methods to the photographic catalogue. For simplicity, a time invariant model is considered:

$$U = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0.90 & 0.85 & 0 & 0 & 0 \\ 0 & 0.12 & 0.71 & 0 & 1 \\ 0 & 0 & 0.29 & 0 & 0 \\ 0 & 0 & 0 & 0.85 & 0 \end{bmatrix}$$

$$F = \begin{bmatrix} 0 & 0 & 0.13 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix}$$

Pathways among stages

The fundamental matrix

What happens during the lifespan of an individual? Which are the possible pathways among stages? We can answer through the fundamental matrix.

Let us consider an individual starts in a transient state j. As time passes, it will visit other transient states, repeating some, skipping others, until it eventually dies.

Stage-structured matrix population model
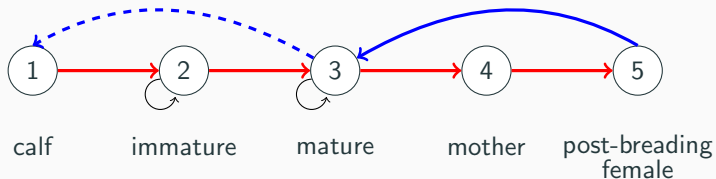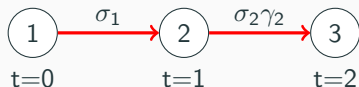

Let ν_{ij} denote **the number of visits to transient state i** that an individual, starting in transient state j, makes **before being absorbed.**

The ν_{ij} are random variables, reflecting individual stochasticity.

The fundamental matrix

Consider an individual who:

- in $t = 0$ is in stage 1 (calf);
- in $t = 1$ transits to stage 2 (immature);
- in $t = 2$ transits to stage 3 (immature);

Since the events are independent, the probability of being in stage 3 is given by the product of the two transition probabilities:

$$\mathbb{P}(stage1 \rightarrow stage2) * \mathbb{P}(stage2 \rightarrow stage3) = \sigma_1 * \sigma_2\gamma_2 =$$
$$= \mathbf{u}_{2,1} * \mathbf{u}_{3,2} = 0.90 * 0.12 = 0.108 \tag{2}$$

The fundamental matrix

$$U^2 = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0.90 & 0.85 & 0 & 0 & 0 \\ 0 & 0.12 & 0.71 & 0 & 1 \\ 0 & 0 & 0.29 & 0 & 0 \\ 0 & 0 & 0 & 0.85 & 0 \end{bmatrix} X \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0.90 & 0.85 & 0 & 0 & 0 \\ 0 & 0.12 & 0.71 & 0 & 1 \\ 0 & 0 & 0.29 & 0 & 0 \\ 0 & 0 & 0 & 0.85 & 0 \end{bmatrix} =$$

$$= \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0.765 & 0.7225 & 0 & 0 & 0 \\ 0.108 & 0.1872 & 0.5041 & 0.85 & 0.71 \\ 0 & 0.0348 & 0.2059 & 0 & 0.29 \\ 0 & 0 & 0.2465 & 0 & 0 \end{bmatrix}$$

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The fundamental matrix

The entries of the matrix $\mathbf{U}$ give the probabilities of visiting each of the transient states after *one time step*.

$\mathbf{U}^2$ gives the probabilities of visiting each of the transient states after *two time steps*.

$\mathbf{U}^3$ gives the probabilities of visiting each of the transient states after *three time steps*.

And so on..

The fundamental matrix

If we add up $\mathbf{U}$ and $\mathbf{U}^2$, each entries represents the probability of visiting a given stage at $t+1$ plus the probability of visiting the same stage at $t+2$.

Proceeding in this way, adding up the powers of $\mathbf{U}$, we get the probabilities of visiting that states over a life time (expected number of visits to each transient state)

In matrix form:

$$\mathbf{N} = E(\nu_{ij}) = \sum_{t=0}^{\infty} \mathbf{U}^t = (\mathbf{I} - \mathbf{U})^{-1}$$

The fundamental matrix

$$N = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 5.88 & 6.52 & 0 & 0 & 0 \\ 16.35 & 18.11 & 22.94 & 19.49 & 22.94 \\ 4.74 & 5.25 & 6.65 & 6.65 & 6.65 \\ 4.02 & 4.46 & 5.65 & 5.65 & 6.65 \end{bmatrix}$$

On average, a calf will spend 1 year as a calf, 5.88 years as a juvenile, 16.3 years as a mature but non-breeding female, etc.

n_{4j} is the expected number of reproductive events that a whale in stage j will experience during her remaining lifetime. Based on this model, a newborn calf could expect to give birth 4.74 times. A mature female could expect to give birth 6.65 times; the difference reflects the likelihood of mortality between birth and maturity.

Life expectancy

Life expectancy

The **longevity of an individual** is the **sum of the time spent in all of the transient states before death**:

$$\eta_j = \sum_i \nu_{ij} \tag{3}$$

where η_{ij} denotes the longevity of an individual currently in stage j.

Life expectancy

The vector of of expected longevities $E(\eta)$, or life expectancies, can be obtained by summing the columns of N:

$$E(\eta^T) = \mathbf{e}^T \mathbf{N} = \begin{bmatrix} 1 & 1 & 1 & 1 & 1 \end{bmatrix} \begin{bmatrix} 1 & 0 & 0 & 0 & 0 \\ 5.88 & 6.52 & 0 & 0 & 0 \\ 16.35 & 18.11 & 22.94 & 19.49 & 22.94 \\ 4.74 & 5.25 & 6.65 & 6.65 & 6.65 \\ 4.02 & 4.46 & 5.65 & 5.65 & 6.65 \end{bmatrix} =$$

$$= \begin{bmatrix} 32.43 & 34.92 & 35.32 & 31.87 & 36.32 \end{bmatrix}$$

Life expectancy of the stages differ only about 15% because mortality rate vary little among stages.

If birth corresponds to stage 1, then life expectancy at birth is:

$$E(\eta_1) = \mathbf{e}^T \mathbf{N} \mathbf{e}_1 \tag{4}$$

where $\mathbf{e}_1$ is a vector with 1 in the first entry and zeros elsewhere.

$$E(\eta_1) = \begin{bmatrix} 32.43 & 34.92 & 35.32 & 31.87 & 36.32 \end{bmatrix} \begin{bmatrix} 1 \\ 0 \\ 0 \\ 0 \\ 0 \end{bmatrix} = 32.43 \tag{5}$$

Variance in life expectancy

Individuals differ in life expectancy because they experience different pathways from birth to death. Longevity can be thought as a random variable, whose variability is a measure of individual stochasticity.

$$V(\eta^T) = e^T N(2N - I) - E(\eta^T) \circ E(\eta^T) \tag{6}$$

For the right whale, the variance and standard deviation of longevity are given by:

$$V(\eta) = \begin{bmatrix} 1157 & 1167 & 1171 & 1163 & 1171 \end{bmatrix} \tag{7}$$

$$SD(\eta) = \begin{bmatrix} 34.0 & 34.2 & 34.2 & 34.1 & 34.2 \end{bmatrix} \tag{8}$$

Variance in life expectancy

So far we have computed life expectancy:

$$E(\eta^T) = \begin{bmatrix} 32.43 & 34.92 & 35.32 & 31.87 & 36.32 \end{bmatrix}$$

and the respective standard deviations:

$$SD(\eta) = \begin{bmatrix} 34.0 & 34.2 & 34.2 & 34.1 & 34.2 \end{bmatrix} \tag{9}$$

Stage-classified models lead to an age-independent mortality rate and life expectancy must be interpreted with care. For instance, life expectancy at birth is 32 years and has a standard deviation of about 34 years. Usually, we expect to find 68 % of the data values within one standard deviation of the mean but in this case it is unlikely to find individuals even at one standard deviation from the mean.

Perturbation analysis

Perturbation analysis

The behaviour of any model depends on the values of its parameters. Perturbation analysis asks **how changes in those parameters will affect** that behaviour. The results of perturbation analysis are often expressed as:

- *sensitivities:* the sensitivity of y to x is the derivative $\frac{dy}{dx}$;
- *elasticities:* the elasticity of y to x is $\frac{x}{y}\frac{dy}{dx}$.

Sensitivity analysis

A **sensitivity analysis** of model parameters determines the **absolute contribution of each demographic parameter** to a given rate (e.g. population growth rate).

It reveals how very small changes in a parameter will affect the rate of interest when the other elements in the matrix are held constant.

Elasticity analysis

One challenge in interpreting sensitivities is that demographic variables are measured in different units. Survival rates are probabilities and they can only take values between 0 and 1. The number of reproductive events, on the other hand, has no such restrictions. This is where elasticity comes into play. **Elasticity analysis** estimates the effect of a **proportional change** in the transition probabilities.

You can directly compare elasticities among all life history variables.

Perturbation Analysis - Life expectancy

Elasticity of life expectancy

Elasticity of life expectancy (calf)
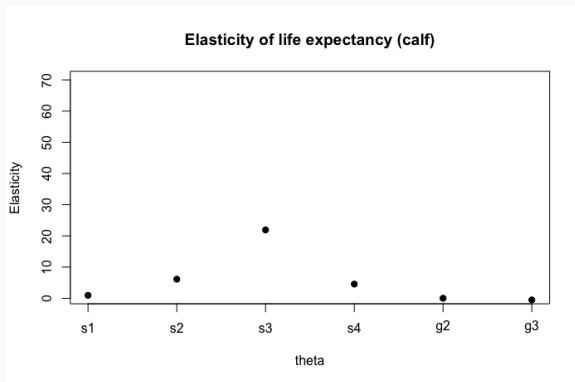
Life expectancy is most elastic to mature female survival σ_3, and less so to σ_2 and σ_4. This partly reflects the longer amount of time spent as a mature female, compared to an immature female or mother. The elasticity to the birth rate γ_3 is negative (-0.61), because of the reduced survival of mothers. A 1% increase in γ_3 will lead to a 0.61% decrease in life expectancy.
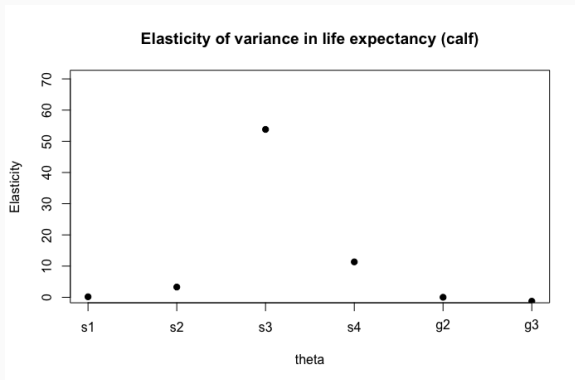
The elasticities of the variance of longevity of a calf is increased by increases in σ_3, less so by increases in σ_2 and σ_4. The pattern of the elasticities is strikingly similar to that of the elasticities of life expectancy.

Perturbation Analysis - Fundamental matrix

Sensitivity of the fundamental matrix

Let θ be a ($p \times 1$) vector of parameters on which the entries of the transition matrix **U** depend.

$$\theta^T = \begin{bmatrix} \sigma_1 & \sigma_2 & \sigma_3 & \sigma_4 & \gamma_2 & \gamma_3 \end{bmatrix} \tag{10}$$

The sensitivity of the fundamental matrix is given by:

$$\frac{dvec\mathbf{N}}{d\theta^T} \tag{11}$$

In our example, this will be a (25×6) matrix.

From sensitivity to elasticity

It is possible to convert a matrix of sensitivity into a matrix of elasticity. In our example:

$$diag(vec\mathbf{N})^{-1} \frac{dvec\mathbf{N}}{d\theta^T} \, diag(\boldsymbol{\theta}) \tag{12}$$

Example. Elasticity of the expected lifetime number of reproductive events

One output of particular interest is the expected number of reproductive events for a calf, i.e. how many times we expect a calf to give birth to a new individual. We can explore the sensitivity of this output with respect to the vector of parameters $\boldsymbol{\theta}$.

We can compute the elasticity of $E(\nu_{41})$ with respect to:

- the survival probabilities $\sigma_1, ..., \sigma_5$;
- the maturation probability γ_2;
- the breeding probability γ_3.

Elasticity of reproductive events

Elasticity of lifetime reproductive events
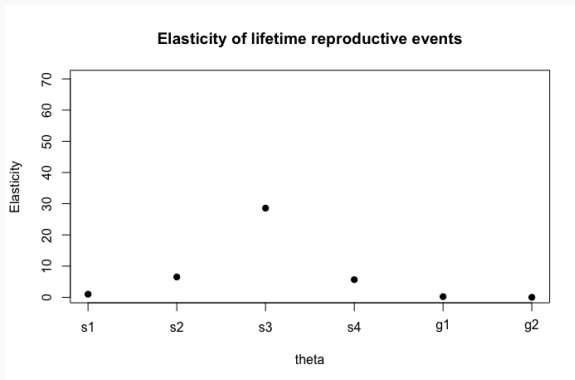
The number of breeding events is most elastic to mature female survival (σ_3), and less so to the survival of immature females or mothers (σ_2 and σ_4). Changes in the probability of giving birth, γ_3, have, remarkably enough, no impact on the expected number of reproductive events.

Variance of the fundamental matrix

Variance of the fundamental matrix

The number of visits to any transient state is a random variable; the fundamental matrix N gives its mean.

The matrix of variances can be computed as:

$$\mathbf{V} = (V(\nu_{ij})) = (2\mathbf{N}_{diag} - \mathbf{I})\mathbf{N} - \mathbf{N} \circ \mathbf{N} \tag{13}$$

The standard deviations of the number of visits to transient states are the square roots of the elements of **V**.

Variance of the fundamental matrix

Each entry in the matrix of variances must be thought as the **result of luck, not heterogeneity.** In other words, each entry represents the variance among a group of individuals all experiencing exactly the same stage-specific transition and mortality probabilities in U.

These values provide a null model for studies of heterogeneity in quantities such as the number of reproductive events.

Elasticity of variance in lifetime reproductive events
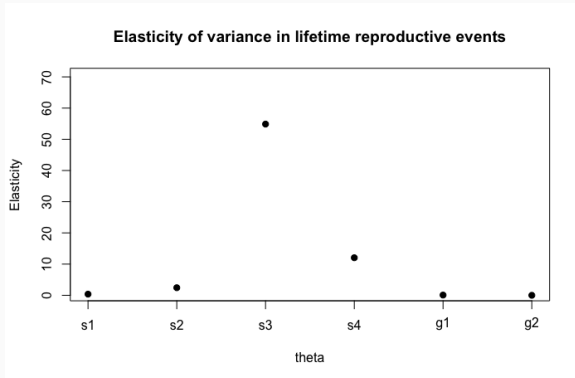
The net reproductive rate

The net reproductive rate

The net reproductive rate R_0 measures lifetime reproductive output (same R_0 of epidemiology, where it measures the potential of a disease to spread). The net reproductive rate satisfies three conditions:

1. R_0 measures the expected lifetime production of offspring;
2. R_0 measures the rate of increase per generation (in contrast to the rate of increase per unit of time, which is given by λ or r);
3. If $R_0 > 1$ then an individual will, on average, produce more than enough offspring to replace itself, the next generation will be larger than the present generation, and the population will grow.
   If $R_0 < 1$, each generation is smaller than the one before, and the population will decline to extinction.

The net reproductive rate

Cushing and Yicang (1994) define R_0 as the per-generation growth rate, given by the dominant eigenvalue ρ of FN:

$$R_0 = \rho[\mathbf{FN}] \tag{14}$$

If only a single type of offspring is produced (call it stage 1), R_0 satisfies the three conditions above.

The net reproductive rate

The right whale produces only a single type of offspring. The generation growth matrix:

$$FN = \begin{bmatrix} 2.13 & 2.35 & 2.98 & 2.54 & 2.98 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{bmatrix} \tag{15}$$

The dominant eigenvalue of FN is its (1, 1) entry :

$$R_0 = \sum_j f_{1j} E(\nu_{j1}) = 2.13 \tag{16}$$

The net reproductive rate

It is interesting to compare $R_0 = 2.13$ with $E(\nu_{41}) = 4.74$. Only female offspring are counted in R_0, whereas $E(\nu_{41})$ counts reproductive events regardless of the sex of the offspring produced. Still, R_0 is less than half of $E(\nu_{41})$, because of the less than perfect survival of calves from $t = 0$ to $t = 1$.

Perturbation Analysis - Net Reproductive Rate

Sensitivity of the Net Reproductive Rate
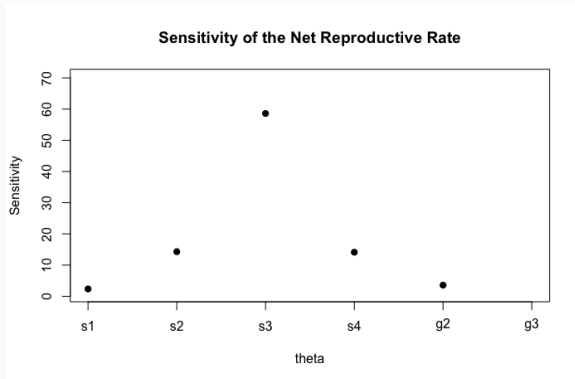
Variable environments

Variable environments

So far we have consider a constant environment. How can we model an environment that varies over time?

- **deterministic aperiodic environments:** fixed historical sequence (e.g. of vital rates);
- **periodic environments:** seasonal variation or seasonal events such as floods, hurricanes, etc;
- **stochastic i.i.d environments:** successive states are drawn independently from a fixed probability distribution;
- **markovian stochastic environments:** the probability distribution of the next environmental state may depend on the current state.

Period and cohort calculations

Period calculations

Conditions of year t are maintained indefinitely and then compared to conditions for $t + 1$. Time-invariant calculations are applied to vital rates of each year and then results are tabulated.

Cohort calculations

Cohort calculations are more realistic: an individual spends its first year of life under the conditions of year t, its second year under the conditions of $t + 1$, and so on. Cohort calculations must account for all the possible environmental sequences through which a cohort may pass.

Matrix U and N for variable environment

The transient matrix **U** is a time-varying matrix **U(t)**. The fundamental matrix becomes:

$$\mathbf{N} = \mathbf{I} + \mathbf{U(0)} + \mathbf{U(1)U(0)} + \mathbf{U(2)U(1)U(0)} + ... \qquad (17)$$

Important: there will be a different matrix **N** for each possible environmental sequence.

Transient matrix U for a given environment

Consider q environmental states: $\varepsilon = 1, ..., q$ and s stages: $g = 1, ..., s$.

If we consider a given environment i, we can construct the transient matrix U_i which represents the possible transition among states, i.e. has dimension $(s \times s)$.

Assemble all the matrices U_i into a block-diagonal matrix:

$$\mathbb{U} = \begin{bmatrix} \mathbf{U}_1 & & \\ & & \\ & & \mathbf{U}_q \end{bmatrix} \tag{18}$$

Transition matrix among environmental states

The transitions among environmental states are defined by a ($q \times q$) column-stochastic matrix D. Use the matrix D to construct a block-diagonal environmental transition matrix of dimension ($sq \times sq$):

$$\mathbb{D} = \begin{bmatrix} \mathbf{D} & 0 & ... & 0 & 0 \\ 0 & \mathbf{D} & ... & 0 & 0 \\ 0 & ... & .. & ... & 0 \\ 0 & ... & ... & ... & \mathbf{D} \end{bmatrix} \tag{19}$$

Aperiodic deterministic environment

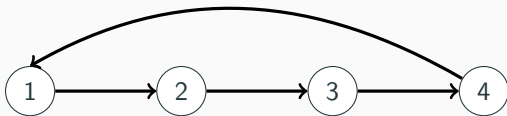In a periodic deterministic environment:
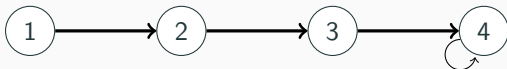
D is defined as:

$$\mathbf{D} = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 1 \end{bmatrix}$$

Periodic deterministic environment

In a periodic deterministic environment:

D is defined as:

$$\mathbf{D} = \begin{bmatrix} 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 \end{bmatrix}$$

i.i.d environment and Markovian environment

In i.i.d environment models, environment i occurs with probability π_i :

$$\mathbf{D} = \begin{bmatrix} \pi_1 & \pi_1 & \pi_1 & \pi_1 \\ \pi_2 & \pi_2 & \pi_2 & \pi_2 \\ \pi_3 & \pi_3 & \pi_3 & \pi_3 \\ \pi_4 & \pi_4 & \pi_4 & \pi_4 \end{bmatrix} \tag{20}$$

In a Markovian environment, D is a column stochastic transition matrix describing the transition probabilities.

Transition matrix

When we consider changing environment, the transition matrix is computed as:

$$\tilde{\boldsymbol{U}} = \mathbb{D}\boldsymbol{K}_{s,q}\mathbb{U}\boldsymbol{K}_{s,q}^{T} \qquad (21)$$

This transition matrix incorporates the transition within each environment and the time variation among environments.

Conclusion

Main points

- Exploiting Markov Chains embedded within a population projection matrix we were able to extract age-classified information from a stage-classified model;

- Individual trajectories are treated as stochastic realization of an underlying stochastic process;

- Perturbation analysis allows to identify how the outputs vary to changes in the parameters: from a conservation and management perspective, analytical sensitivity analysis can help you identify the stage that will contribute the most to population growth of a species.

- Individual stochasticity can be considered as a null model for study of individual heterogeneity (e.g. frailty);

Thank you!