Appendix IV – descriptors of the transient dynamics

The linear combination (linear in the parameters) of the eigenvalues, eigenvectors and c coefficients extracted from the demographic matrix estimates the population vector at any given time t. Hence, these metrics define the properties of the transient trajectory, namely its initial momentum, duration and wave period and amplitude. Most of this is approached on the literature about matrix population dynamics, as are the cases of Caswell (1987 and 2001) and Tuljapurkar and Caswell (1997). A brief overview is followed in order to better understand the complex dynamics that govern the transient phase and its relationship with the demography of algae with biphasic life cycles.

Central tendency

The long-term population dynamics are given by the dominant set, that is: the long-term growth rate tends asymptotically to the dominant eigenvalue and the long-term population structure is given by the eigenvector associated to it. Thus, any statistic from the long-term population structure, as is the H:D, can be estimated upon this eigenvector (Vieira and Santos 2010) . As this dominant eigenvalue is strictly real and positive, growth or decline is monotonical and the population structure is stable. During the transient phase the dominant eigenvalue is the central value around which oscillates the growth rate at a given time t, but it is not its actual rate. Likewise, the associated eigenvector gives the central tendency of the population structure, but it is not its actual structure. Thus, any statistic estimated upon this eigenvector is the central tendency upon which the actual values of the statistic oscillate (Fig.1).

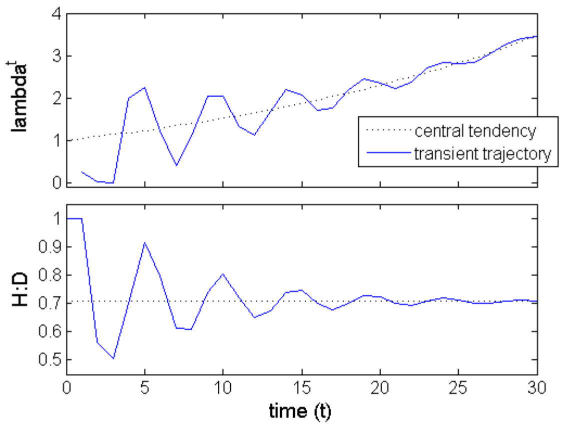

Figure 1 – (a): λ trajectory; (b) H:D trajectory; λ_a = 1.042; $\lambda_{b,c}$=0.218±0.869i; abs($\lambda_{b,c}$)=0.9; $\theta_{b,c}$ = ±1.325rad = ±75.9º; wave period = 4.74; persistence rate=0.86.

Persistence rate

For each of the sets of eigenvalue, eigenvector and c coefficient, exponential growth or decline depends only on each eigenvalue being bigger or smaller than 1 in absolute value. Relative to the higher all the smaller eigenvalues tend to turn negligible and thus their influence in the population dynamics fades away (Fig.1). The rate at which the transient phase fades away is commonly measured by the "damping ratio" between the magnitudes of the biggest (dominant) and the second biggest (sub-dominant) eigenvalues ($|\lambda_a|/|\lambda_b|$). The closer it is to 1 the more the transient phase prevails, but it may raise to $+\infty$. Presently, this statistic was inverted to $|\lambda_i|/|\lambda_a|$ and named the "persistence rate". With this inversion all eigenvalues are scaled to the dominant and their persistence rates are comprised within the 0 to 1 range. Higher non-dominant eigenvalues, closer to the dominant, have a persistence rate closer to 1 and will take longer to fade away. Moderate non-dominant eigenvalues have a moderate persistence rate and will fade away quicker. Small non-dominant eigenvalues have a persistence rate closer to 0 and will be almost imperceptible. It also enables to estimate the dissipation rate as 1-'persistence rate'. The persistence rate and the dissipation rate are direct measures of the rate at which the initial momentum (given by the c_i coefficients) of each eigenvector prevails or dissipates. Therefore, it was fundamental to adopt the persistence rate instead of the damping ratio.

Oscillation period

Eigenvalues vary independently as they are raised to time t. Real positive eigenvalues show monotonical exponential growth or decline whether they are bigger or smaller than 1. Real negative eigenvalues oscillate between positive and negative values with a period of 2 (fig.2). Complex eigenvalues cycle through the complex plane with a period of $2\pi/\theta$ (fig.3 left). However, complex sets of eigenvalue, eigenvector and c coefficient always come in complex conjugate pairs which, when combined, cancel out their imaginary components. Thus the sum of the complex conjugate eigenvalues oscillates between strictly real positive and negative values with the same period of $2\pi/\theta$ (fig.3 right). The oscillation period (or wave length) of the transient trajectory is given by the sub-dominant eigenvalue. Nevertheless, if other eigenvalues have approximate magnitudes it is over-imposed different cycles leading to an oscillation pattern that resembles chaotic.

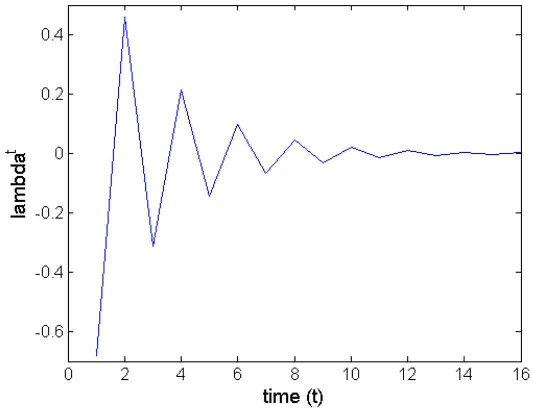

Fig.2 – Oscillatory trajectory of a strictly real negative eigenvalue; λ_b=-0.68; θ_b=180º; wave period=2.

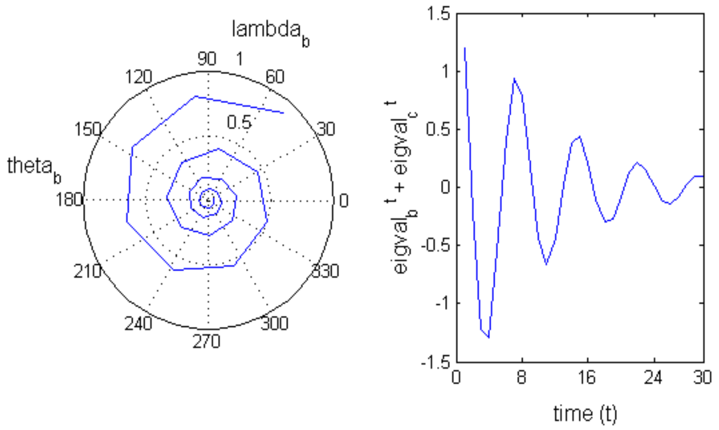

Figure 3 –Oscillatory trajectory of (left) a complex eigenvalue; λ_b=0.598+0.679i; abs(λ_b)=0.905; θ=48.6º; wave period=7.41. (right) the complex conjugated pair of eigenvalues λ_b and λ_c.

Population structure

At any time t the central tendency of the population structure is given by the eigenvector (w_a) associated to the dominant eigenvalue (λ_a), which includes only real, non-negative values. The other eigenvectors (w_i for $i \neq a$) give the residuals that add up to the central tendency yielding the actual population structure. The sum of the residuals is the wave amplitude. The relative weights of the central tendency and residuals for a given time t are given by $c_i|\lambda_i|^t$. These weights represent the actual momentum of w_i at time t.

The bulk of the oscillatory pattern is given by the sub-dominant set of eigenvector, eigenvalue and c coefficient (or complex conjugated pair of eigenvectors, eigenvalues and c coefficients), whereas the smaller ones may yield smaller, usually undetectable oscillations around the main oscillating trajectory (fig.1). Nonetheless, several of the biggest non-dominant sets may have approximate absolute values for their eigenvalues, eigenvectors and c coefficients, leading to over-imposed oscillations of close magnitude but different periods (figs 4). The resulting transient trajectory is odd. However, a statistic like the H:D, by averaging over stage classes, tends to smooth it.

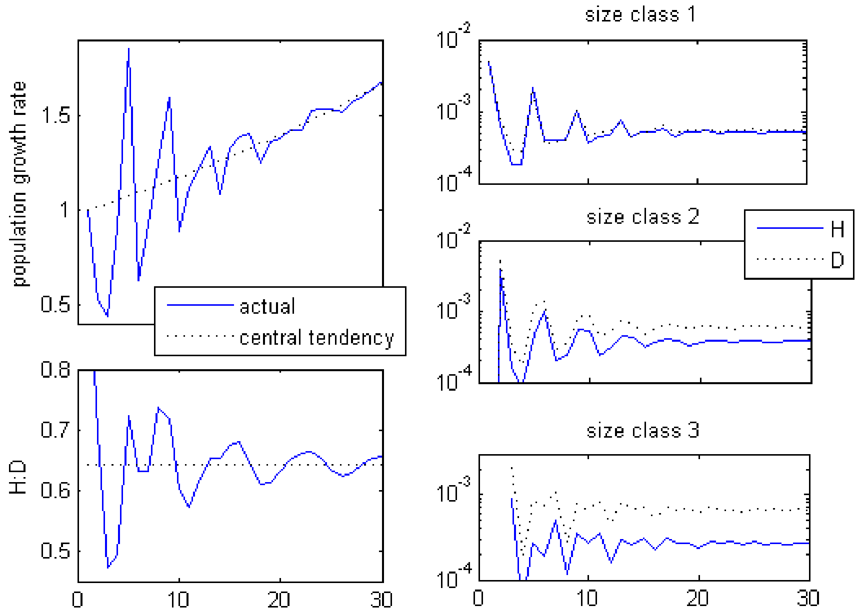

Fig.4 – $Eigval_a$=1.02, λ_a=1.02 and θ_a=0. $Eigval_{b,c}$=-0.07±0.83i, $\lambda_{b,c}$=0.83, persistence $rate_{bc}$=0.81, $\theta_{b,c}$=±95.1° and wave $period_{(b,c)}$=3.79; $eigval_d$=-0.85, λ_d=0.85, persistence $rate_{bc}$=0.83, θ_d=180° and wave $period_{(d)}$=2.

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Initial conditions and momentum

The c coefficients define how much of the initial population structure is explained by each eigenvector. So, by weighting the eigenvalues and eigenvectors they also weight their influence in the transient phase because the population's trajectory carries a memory of the initial conditions, which fades away as time goes by (figures 1, 4 and 5). This memory is the momentums the eigenvectors bear at any particular time. The initial momentum of each eigenvector is given by its c coefficient. The rate at which it grows or decays is given by the correspondent eigenvalue. In relative terms, each relative initial momentum is given by $\gamma_b/\sum\gamma_i$ for the real sets or $2\gamma_b/\sum\gamma_i$ for the complex conjugate sets (see equation 3 in the bulk article). The rate at which the momentum prevails is given by the persistence rate ($|\lambda_b|/\lambda_a$). Hence, at any time t the prevailing relative momentum is given by $\gamma_b/\sum\gamma_i*(|\lambda_b|/\lambda_a)^t$ for the real sets and $2*\gamma_b/\sum\gamma_i*(|\lambda_b|/\lambda_a)^t$ for the complex conjugate sets. In particular situations there may be a c coefficient close to zero that cancels out its associated eigenvector. If the correspondent eigenvalue is the sub-dominant it will transfigure the population's trajectory, altering the otherwise expected duration, period and amplitude of the transient phase.

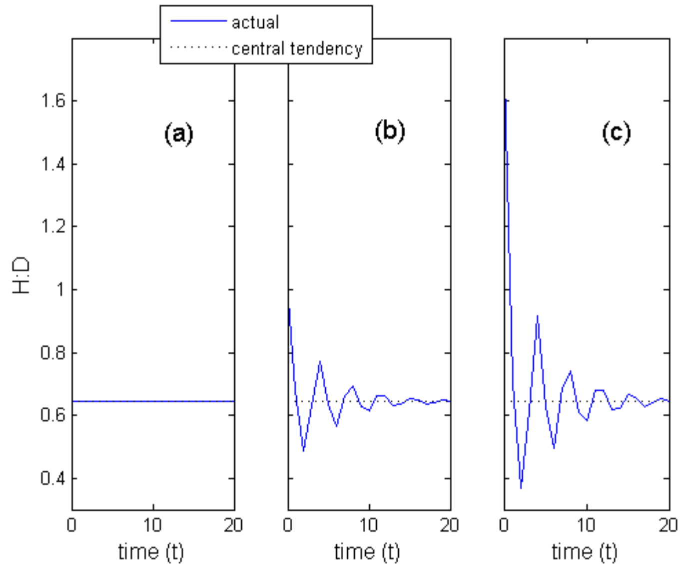

Fig.5 – H:D when the c coefficients for the complex conjugated pair were multiplied (a) by 0, (b) by 1 and (c) by 2.