To understand the effect of the projection interval on the dynamics of a population, one must examine the underlying nature of the projection process.

This quickly takes us into the world of **transient dynamics** which can differ markedly from equilibrium expectations

The precise dynamics of the matrix projection $\mathbf{n_t} = \mathbf{A^t} \times \mathbf{n_0}$ can be seen by examining the equivalent summation equation:

$$\mathbf{n_t} = \sum_{\mathbf{i}} \lambda_{\mathbf{i}}^{\mathbf{t}} \times \mathbf{w_i} \times \mathbf{c_i}$$

where

$\lambda_{\mathbf{i}}$ is the ith eigen value of the matrix **A**

$\mathbf{w_i}$ is the ith associated eigen vector

$\mathbf{c_i}$ is the ith scalar element found as $\mathbf{c} = \mathbf{W}^{-1} \times \mathbf{n}_0$

and

W is the matrix of eigen vectors

$\mathbf{n_0}$ is again the initial age vector

If we consider an i=3 stage class model, this is simply expanded for the first 2 years as:

$$\mathbf{n}_1 = \left(\lambda_1^1 \times \mathbf{w}_1 \times \mathbf{c}_1\right) + \left(\lambda_2^1 \times \mathbf{w}_2 \times \mathbf{c}_2\right) + \left(\lambda_3^1 \times \mathbf{w}_3 \times \mathbf{c}_3\right)$$

$$\mathbf{n}_2 = \left(\lambda_1^2 \times \mathbf{w}_1 \times \mathbf{c}_1\right) + \left(\lambda_2^2 \times \mathbf{w}_2 \times \mathbf{c}_2\right) + \left(\lambda_3^2 \times \mathbf{w}_3 \times \mathbf{c}_3\right)$$

To see how the relative contributions of the 3 terms to n_t change as t increases, we can use our matrix A from before and an initial age distribution of n_0 = [1/3 1/3 1/3]'. We find the terms we need as:

$$\lambda = \left[1.01 \quad -0.15 + 0.21\mathbf{i} \quad -0.15 - 0.21\mathbf{i}\right]'$$

$$\mathbf{W} = \begin{bmatrix} 0.50 & -0.17 + 0.23\,\mathbf{i} & -0.17 - 0.23\,\mathbf{i} \\ 0.35 & 0.75 & 0.75 \\ 0.79 & -0.58 + 0.14\,\mathbf{i} & -0.58 - 0.14\,\mathbf{i} \end{bmatrix}$$

$$\mathbf{c} = \left[0.59 + 0.00\,\mathbf{i} \quad 0.08 - 0.14\,\mathbf{i} \quad 0.08 - 0.14\,\mathbf{i}\right]'$$

$$\mathbf{n}_1 = \underbrace{\left(\lambda_1^1 \times \mathbf{w}_1 \times \mathbf{c}_1\right)}_{\text{term 1}} + \underbrace{\left(\lambda_2^1 \times \mathbf{w}_2 \times \mathbf{c}_2\right)}_{\text{term 2}} + \underbrace{\left(\lambda_3^1 \times \mathbf{w}_3 \times \mathbf{c}_3\right)}_{\text{term 3}}$$

time = 1	term1	term 2	term 3	sum
age class 1	0.3026	-0.0113 – 0.0029i	-0.0113 + 0.0029i	0.2800
age class 2	0.2098	0.0118 + 0.0291i	0.0118 - 0.0291i	0.2333
age class 3	0.4739	-0.0036 – 0.0247i	-0.0036 + 0.0247i	0.4667

time = 2	term1	term 2	term 3	sum
age class 1	0.3056	0.0024 – 0.0019i	0.0024 + 0.0019i	0.3103
age class 2	0.2118	-0.0079 + 0.0020i	-0.0079 - 0.0020i	0.1960
age class 3	0.4785	0.0057 + 0.0031i	0.0057 - 0.0031i	0.4900

time = 10	term1	term 2	term 3	sum
age class 1	0.3306	0	0	0.3306
age class 2	0.2292	0	0	0.2292
age class 3	0.5177	0	0	0.5177

time = 10	term1	term 2	term 3	sum
age class 1	0.3306	0	0	0.3306
age class 2	0.2292	0	0	0.2292
age class 3	0.5177	0	0	0.5177

If we re-scale the last column so it sums to 1, we find n_{10} = [0.3068 0.2127 0.4805] which is identical to the stable age distribution extracted as the dominant eigen vector given as column 1 in the matrix **W** (once it is also re-scaled to sum to 1).

We also find that the population is growing at λ = 1.01, the value of λ_1 the dominant eigen value.

What has happened?

$$\mathbf{n}_1 = \left(\lambda_1^1 \times \mathbf{w}_1 \times \mathbf{c}_1\right) + \left(\lambda_2^1 \times \mathbf{w}_2 \times \mathbf{c}_2\right) + \left(\lambda_3^1 \times \mathbf{w}_3 \times \mathbf{c}_3\right)$$

term 1 term 2 term 3

During the first few years, all 3 terms made contributions to the numbers of individuals in each of the 3 age classes.

As time increased, the effect of the terms associated with all but the dominant eigen value declined and converged to 0.

These other eigen values are formally called the sub-dominant eigen values and they contribute to the transient dynamics of the system.

If a population projection begins at anything other than its expected stable age distribution, the sub-dominant eigen values affect growth until the stable age distribution is reached.

Once that occurs, equilibrium theory takes over and we can simply rely on growth estimated as the dominant eigen value λ_1.

If the population begins at the stable age distribution, then the scalars c_i are simply [1 0 0] and terms 2 and 3 above become 0 immediately, regardless of the magnitude of the sub-dominant eigen values.

A more general understanding of the decreasing importance of the terms involving the sub-dominant eigen values can be seen if we take the expanded form of the equation for n_t

$$\mathbf{n_t} = \left(\lambda_1^t \times \mathbf{w_1} \times \mathbf{c_1}\right) + \left(\lambda_2^t \times \mathbf{w_2} \times \mathbf{c_2}\right) + \left(\lambda_3^t \times \mathbf{w_3} \times \mathbf{c_3}\right) + \ldots$$

dividing through by λ^t_1 we obtain

$$\frac{\mathbf{n_t}}{\lambda_1^t} = \left(\mathbf{w_1} \times \mathbf{c_1}\right) + \left(\left(\frac{\lambda_2}{\lambda_1}\right)^t \times \mathbf{w_2} \times \mathbf{c_2}\right) + \left(\left(\frac{\lambda_3}{\lambda_1}\right)^t \times \mathbf{w_3} \times \mathbf{c_3}\right) + \ldots$$

The Perron Frobenius theorem assures us that for primitive matrices of the type normally encountered in population projections that there will be 1 dominant eigen value whose magnitude is larger than the others such that $\lambda_1 > \{ |\lambda_2|, |\lambda_3|, \ldots\}$. Given this, the limit of the previous equation is:

$$\lim_{t \to \infty} \frac{\mathbf{n_t}}{\lambda_1^t} = \mathbf{w_1} \times \mathbf{c_1}$$

Note that all terms not involving λ_1 have disappeared.

This is the strong ergodic theorem which shows that the long-term dynamic of a population are controlled by the dominant eigen value and its associated dominant eigen vector.

But what happens if we are not interested in just long-term dynamics?

What happens over the short-term? Especially over the time frame of most management programs.

The duration of transient behavior ultimately depends on the relative magnitudes of the set of eigen values.

Transient behavior continues until all of the $\lambda^{\mathbf{t}}_{\mathbf{i}}$ = 0 for all but λ_1 the dominant eigen value.

The eigen values are an emergent property of the Levkowitch matrix and ultimately the life history of the critter.

Re-examining the projection, we see that other terms affect the pattern of the transient behavior.

$$\mathbf{n_t} = \left(\lambda^{\mathbf{t}}_{\mathbf{1}} \times \mathbf{w_1} \times \mathbf{c_1}\right) + \left(\lambda^{\mathbf{t}}_{\mathbf{2}} \times \mathbf{w_2} \times \mathbf{c_2}\right) + \left(\lambda^{\mathbf{t}}_{\mathbf{3}} \times \mathbf{w_3} \times \mathbf{c_3}\right) + \ldots$$

Early behavior depends on the associated eigen vectors $\mathbf{w_i}$ which are again a property of life history.

More critically, early transient behavior depends on the $\mathbf{c_i}$ terms which are a function of both the initial age distribution and inverse of **W**, again a property of the life history related to age-specific reproductive success.

The life history of a particular critter is fixed by its evolutionary history.

The initial age distribution, however, is the aspect which raises some of the more profound management issues – especially since management actions are always short-term but rely on long-term equilibrium projections.

Imagine a population that is near its stable age distribution.

Imagine further that some event kills a proportion of that population but does so in a way that is not random with respect to age distribution.

For example, consider a species that has a 1-year delay in the onset of breeding and for which all the non-breeding individuals congregate in a single area (say a bay in the Beaufort Sea near the Arctic National Wildlife Refuge) and suppose we have an oil spill.

This **pulse perturbation** selectively reduces one of the age classes below the equilibrium expectation.

It therefore changes the $\mathbf{c_i}$ set and may profoundly impact the transient dynamics that occur over the next few years.

We know virtually nothing about the pattern of these transients.

Our preliminary work shows that a pulse perturbation that reduces the younger age classes leads to short-term dynamics with a higher growth rate than equilibrium expectations.

Conversely, reductions in the relative frequency of older age classes depresses the population growth rate to an extent where local extirpation is possible.

The sad reality is that we do not know much about this.

Our “ignorance” reflects our persistent, blind reliance on equilibrium solutions.

This, in turn, reflects the facts that such solutions are mathematically more tractable and are much simpler to explain to those who make management decisions.

Correcting this requires that we explore these more complex dynamics AND figure out a way to explain the results to (perhaps) well-intentioned managers with limited ability.

I am currently involved in a project that is addressing the first part of this.

The primary player is Dave Koons, a graduate student from Auburn University that am helping to supervise.

With luck (and interest), the EEB program of CUNY can bring Dave here next year to share his findings with all of us.

His supervisor is Barry Grand, one of my colleagues from Alaska and spectacled eider research who recently moved to Auburn to head-up their USGS-BRD cooperative research unit.

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