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A statistical investigation into the properties and dynamics of biological populations experiencing environmental variability

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Chapter 2: Deterministic Models

2.1 Introduction

A substantial amount of literature has, over the years, been dedicated to the modelling of biological populations e.g. Kendall et al. (1999), Marion et al. (2000), Ogutu et al. (2003), and Roughharden (1977). All models can be divided into two broad categories: those that are deterministic in nature and those that are stochastic. The deterministic school has a strong following. Indeed, when stochastic variability is not large, such models often provide great insight into the behaviour of populations. By ignoring the randomness inherent in population behaviour, deterministic models implicitly assume that if we know the present condition of a population, we can predict its future.

All the models described in this chapter are based on transition rates. As mentioned in Chapter 1, there are only four processes that can change the population size: birth, death, immigration and emigration. Many populations have negligible migration rates in which case the population size can only be significantly altered by the births and deaths that occur within. If we define our population of interest to be some biological species then migration would become a meaningless concept. Hence, the migration rates will be zero and the population would only change when a birth or a death occurred. The most well-known deterministic models assume that the birth and death rates are uniquely determined by the current population size, N. Such models are studied in Chapters 2, 3 and 4.

Many models assume (see Matis et al, 2000) that the transition rates are formed by the merging of two primary components:

i. Per capita rates: the resulting increase in the birth and death rates if the population were to increase by one (ignoring population density pressures).
ii. Crowding coefficients: the resulting decrease (increase) in the birth (death) rate owing to the extra density pressure that is exerted on the population were the population to experience a unit increase in size.

One would expect the crowding coefficient to be insignificant when the population is small (since there is little crowding) – hence the per capita rates will be dominant – whilst the crowding coefficient should be large (and hence dominant) when the population is large.

Let B and D be the birth rate and the death rate respectively. The following transition rate model proposed by Matis et al. (2000) is consistent with the above propositions:

$$B(N)=\begin{cases} a_1N-b_1N^{s+1} & \text{for } N<\left(a_1/b_1\right)^{1/s} \\ 0 & \text{otherwise} \end{cases} \qquad \begin{array}{l} \text{where } a_1>b_1,\ a_2>b_2,\ s=1,2,\ldots \\ a_1,a_2,b_1,b_2,s \text{ are constants} \end{array}$$
$$D(N)=\ a_2N+b_2N^{s+1} \qquad (2.1.1)$$

Apart from reflecting the underlying dynamics, the functional form of these transition rates are also reasonably simple. Banks (1994) showed that, when the initial population size is N_0, the transition rates suggested by equation (2.1.1) imply that:

$$N(t)=\left[\frac{\left(\frac{a_1-a_2}{b_1+b_2}\right)}{1+\left(\left(\frac{a_1-a_2}{N_0{}^s\left(b_1+b_2\right)}\right)-1\right)e^{-(a_1-a_2)st}}\right]^{1/s} \qquad (2.1.2)$$

The above model is known as the power-law logistic model. The power-law logistic model is fully characterized by its transition rates and the initial population size, N_0.

One can increase the model's realism by including, in addition to the population size, other dynamically relevant factors. Such factors include:

- the age structure of the population
- the current environmental condition
- the population size of other relevant species

The environmental condition is thought to be an especially useful predictor of the transition rates. Accordingly, it is covered in some detail in the later chapters. Unfortunately, the inclusion of additional factors often causes the resulting differential equations to be unsolvable. One can either try using various methods of approximation to make such differential equations solvable or try to solve such equations numerically.

2.2) Locally linear approximations about the equilibrium state

Ignoring migration, a population can change in size in only two ways: birth and death. Hence, if we assume that the transition rates are dependent only on the population size; and that we can consistently let ΔN and Δt become very small, then the behaviour of the population can be fully encapsulated by a deceptively simple differential equation:

$$\frac{dN}{dt}=B(N)-D(N) \qquad (2.2.1)$$

Equation (2.2.1) is only an approximation since N is treated as a continuous variable.

Unfortunately, the underlying functional forms of the transition rates can make the above differential equation unsolvable. In such cases, we look for a tractable differential equation that approximates the features of equation (2.2.1) to use in inference.

If the transition rates proposed in (2.1.1) are used, then equation (2.2.1) takes on the form:

$$\frac{dN}{dt} = (a_1 - a_2)N - (b_1 + b_2)N^{s+1} \tag{2.2.2}$$

The power-law logistic model given in (2.1.2) is simply the solution of the above differential equation with boundary condition: $N(0) = N_0$.

A number of the calculations performed in this research report make use of the concept of the equilibrium state. By linearizing equation (2.2.1) about such an equilibrium state one will be able to derive an approximate analytical expression for $N(t)$. The details of such a derivation are given below. Sections 2.2 – 2.4 are primarily based on the work of Nisbet et al. (1982). These authors defined a population to be in an equilibrium state, N^*, if, in that state, the population size remains constant. That is:

$$\left.\frac{dN}{dt} = 0\right|_{N=N^*} \tag{2.2.3}$$

If we assume that there is no migration then equation (2.2.3) implies that:

$$B(N^*) = D(N^*) \tag{2.2.4}$$

The equilibrium state is said to be stable if, after experiencing a perturbation, the population ultimately returns to its steady state value. So if the population numbers suddenly increase above N^*, we expect the population to slowly decrease back to its equilibrium state. Similarly, the population should increase towards N^* if the perturbation causes the population size to decrease. This implies that:

$$\begin{aligned} &B(N) < D(N) \quad \text{whenever } N > N^* \\ &B(N) > D(N) \quad \text{whenever } N < N^* \end{aligned} \tag{2.2.5}$$

Conversely, the equilibrium state is said to be unstable if the inequalities are reversed.
A necessary (though not a sufficient) condition for a state to be in stable equilibrium is:

$$\left[\frac{dB}{dN} - \frac{dD}{dN}\right] < 0 \quad \text{when } N = N^* \tag{2.2.6}$$

Equation (2.2.14) illustrates how such a condition ensures that the linearized population model is stable.

A large number of biological populations have a stable equilibrium state (see Hassell et al. (1977)). By making the reasonable assumption that a population will tend towards its stable equilibrium state (as opposed to, say oscillating around the equilibrium state), it follows that the population should be close to equilibrium at any given time. Linear approximations that are centred on such equilibrium states should then be reasonably accurate.

Matis et al. (2000) considered the following transition rates:

$$B(N) = \begin{cases} 0.3N - 0.015N^2 & \text{for } N < 20 \\ 0 & \text{otherwise} \end{cases} \qquad (2.2.7)$$
$$D(N) = 0.02N + 0.001N^2$$

These transition rates are simply a special case of the power-law logistic model. Graphically, these transition rates look as follows:

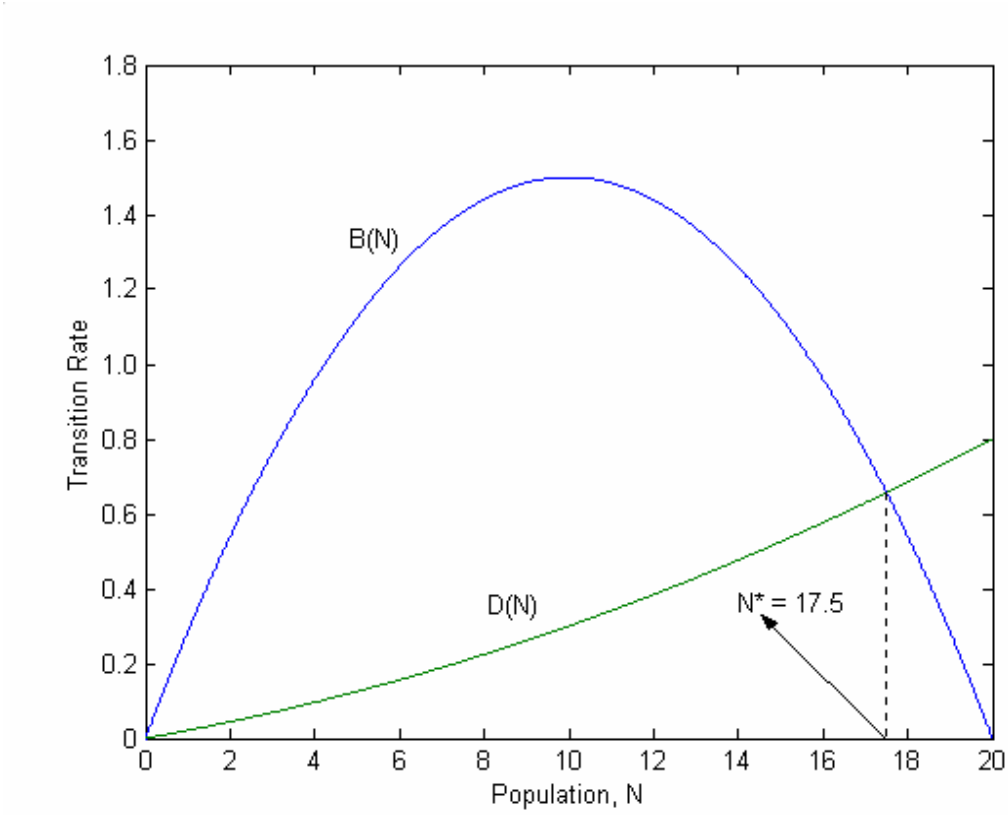


Figure 2.1 Birth and Death transition rates for Equation (2.2.6)

From Figure 2.1, one can see that the population is in equilibrium when $N = 0$ (extinction) as well as when $N = 17.5$. Furthermore, one can see that $B(N) > D(N)$ for $N < 17.5$ and that $B(N) < D(N)$ for $N > 17.5$ so, by equation (2.2.5), we know that $N = 17.5$ is a stable equilibrium state. Thus, when ignoring extinction, the population

should, after any perturbation, tend towards a size a 17.5. Of course, it is absurd to speak of “17.5” animals – the model seems to indicate that, without any perturbations, the population will continuously oscillate between a size of 17 and a size of 18.

Consider a population that is displaced slightly from its stable equilibrium. Let n be the displacement of a population from its equilibrium state. That is:

$$n = N - N^* \tag{2.2.8}$$

Then, by expanding about the steady equilibrium state, we obtain the following differential equations:

$$B(N) = B(N^*) + n\left(\frac{dB}{dN}\right)_{N=N^*} + O(n^2) \tag{2.2.9}$$

$$D(N) = D(N^*) + n\left(\frac{dD}{dN}\right)_{N=N^*} + O(n^2) \tag{2.2.10}$$

where $O(n^2)$ denotes all terms of order n^2 or higher. Substitution of the above equations into equation (2.2.1) yields:

$$\frac{dN}{dt} = \frac{dn}{dt} = \left\{B(N^*) - D(N^*)\right\} + n\left(\frac{dB}{dN} - \frac{dD}{dN}\right)_{N=N^*} + O(n^2) \tag{2.2.11}$$

It follows from equation (2.2.4) that the first term is zero. Also, we expect the terms of order n^2 and above to be very small when n is close to zero. Indeed, terms of order n^2 and above should be quite small for even moderate values of n provided that the transition rates are not highly non-linear. Hence, the higher order terms can be ignored. If in addition, we let:

$$\lambda = \left[\frac{dB}{dN} - \frac{dD}{dN}\right]_{N=N^*} \tag{2.2.12}$$

then equation (2.2.11) simplifies to:

$$\frac{dn}{dt} = \lambda n \tag{2.2.13}$$

If the initial population size is N_0 then equation (2.2.13) has solution:

$$n = \left(N_0 - N^*\right)e^{\lambda t} \tag{2.2.14}$$

Equation (2.2.14) implies that the initial fluctuation will decay exponentially if $\lambda < 0$. If $\lambda > 0$, the population will diverge. Some biological populations that have been studied (see Nisbet et al. (1982)) have a cyclic decay to equilibrium, so the model studied in this section is not suitable for every population.

2.3) Delayed Regulation

The models covered thus far have had the transition rates embodied as functions solely of the current population size, N. The realism of such abstractions is questionable as one would also expect the transition rates for most populations to be dependant on the past history of the population. For example, if population numbers were initially very high and if the population has recently suffered a drastic drop in numbers, then the observed birth rate could be significantly higher than that predicted by the earlier models – A lot of mating could have taken place in the abundant period and, in the lean period, most of the deaths could have been suffered by the very old and very young members of the population (who are incapable of reproduction). Ogutu et al. (2003) found evidence for such delayed regulation for a number of African herbivore populations. We now look at a way to account for this delayed regulation.

Consider a weighted average of previous population numbers, $N_w(t)$. The population at each time-point up to the present is assigned a weight by the weighting function, $w(t)$. So $N_w(t)$ is given by:

$$N_w(t) = \int_0^\infty w(u)N(t-u)du \qquad \text{with } \int_0^\infty w(u)du = 1 \tag{2.3.1}$$

If $w(t)$ is a Dirac function that is centred at 0, then $N_w(t)$ simplifies to N.

If the population growth rate depends on both N and N_w then the population can be modelled as

$$\frac{dN}{dt} = G(N, N_w) \tag{2.3.2}$$

in which case one can linearize about the stable equilibrium state thus obtaining:

$$\frac{dn}{dt} = -an - bn_w \qquad \text{where } a \equiv -\left(\frac{\partial G}{\partial N}\right)_{N=N_w=N^*}, b \equiv -\left(\frac{\partial G}{\partial N_w}\right)_{N=N_w=N^*} \tag{2.3.3}$$
$$n(t) = N(t) - N^*$$

Nisbet et al. (1982) stated that the solution to the above equation has the following form:

$$n(t) \propto e^{-\mu t} e^{i\omega t} \tag{2.3.4}$$

where μ and ω are solutions of the following two simultaneous equations:

$$\mu = a + b\int_0^\infty w(u)e^{\mu u}\cos\omega u\, du \tag{2.3.5}$$

$$\omega = b\int_0^\infty w(u)e^{\mu u}\sin\omega u\, du \tag{2.3.6}$$

I will now consider a specific case of the model given in equation (2.3.3).

2.3.A) Example

Consider the case where the population growth rate, $G(N, N_w)$ has the form:

$$\frac{dN}{dt} = G(N, N_w) = \alpha N - \beta N^2 + \gamma N_w \tag{2.3.7}$$

α, β and γ are positive constants in the above equation. Also let the weighting function, $w(u)$, for the past population numbers have the form:

$$w(u) = \tfrac{1}{T_D} e^{-u/T_D} \quad \text{where } T_D \text{ is the average time delay} \tag{2.3.8}$$

Hence, under equation (2.3.8), recent population numbers have a more significant impact on the future population trajectory than the population numbers in the distant past. We examine the implications these equations have on population behaviour.

Under the proposed weighting function, $N_w(t)$ has the following form:

$$N_w(t) = \int_0^\infty \tfrac{1}{T_D} e^{-u/T_D} N(t-u)du \tag{2.3.9}$$

Nisbet et al. (1982) stated that $n(t) \propto e^{-\mu t} e^{i\omega t}$. This implies that:

$$N(t) = Ce^{-\mu t} e^{i\omega t} + N^* \qquad \text{where } C \text{ is a constant} \tag{2.3.10}$$

If we let $\lambda = -\mu + i\omega$, we have:

$$n(t) \propto e^{\lambda t} \tag{2.3.11}$$

$$N(t) = Ce^{\lambda t} + N^* \tag{2.3.12}$$

Substituting equation (2.3.12) into equation (2.3.9), we then have:

$$\begin{aligned} N_w(t) &= \int_0^\infty \tfrac{1}{T_D} e^{-u/T_D} \left[Ce^{\lambda(t-u)} + N^* \right] du \\ &= \frac{N(t) + \lambda T_D N^*}{1 + \lambda T_D} \end{aligned} \tag{2.3.13}$$

If we then substitute this expression for $N_w(t)$ into equation (2.3.7), we obtain:

$$\frac{dN}{dt} = \left(\alpha + \frac{\gamma}{1+\lambda T_D} \right) N - \beta N^2 + \frac{\gamma \lambda T_D}{1+\lambda T_D} N^* \qquad where\ N^* = \frac{\alpha + \gamma}{\beta} \tag{2.3.14}$$

Applying the definitions given in equation (2.3.3) for a and b, to equation (2.3.14), it follows that a and b are as follows:

$$\begin{aligned} a &= \alpha + \left(2 - \frac{1}{1+\lambda T_D} \right) \gamma \\ b &= \alpha + \gamma + \alpha \lambda T_D + 2\lambda \gamma T_D \end{aligned} \tag{2.3.15}$$

Using the expressions in (2.3.15), one can derive the following expression for λ:

$$\lambda = \frac{-(1 + 2\alpha T_D + 4\gamma T_D) \pm \sqrt{-8T_D(\alpha + \gamma) + (1 + 2\alpha T_D + 4\gamma T_D)^2}}{2T_D} \tag{2.3.16}$$

Cyclic decays are only possible when λ is a complex number. Equation (2.3.4) states that, for complex values of λ, $n(t) \propto e^{-\mu t} e^{i\omega t}$. Using the relationship $e^{i\omega t} = \cos\omega t - i\sin\omega t$, we have $n(t) \propto e^{-\mu t}(\cos\omega t - i\sin\omega t)$. The term $e^{-\mu t}$ ensures that all population displacements decay to zero whilst the $(\cos\omega t - i\sin\omega t)$ causes these decays to be cyclical. It can easily be shown that the term under the square root in equation (2.3.14) is non-negative. Thus – for a model given by equations (2.3.7) and (2.3.8) – λ is always a real number, and hence, equation (2.3.7) is incapable of decaying cyclically to equilibrium. Nisbet et al. (1982) showed, for certain functional forms of $G(N, N_w)$ and $w(t)$, that the model is capable of decaying cyclically to equilibrium after any perturbation whilst under still other parameters and functional forms, the model will decay monotonically towards equilibrium. Thus, by recognizing the delayed response that each member of the population has to its external conditions, a delayed-regulation model is capable of mimicking a wider range of behaviours that a population could possibly exhibit after a perturbation than the power-law logistic model.

Using a result given by Matis et al. (2000), the solution to equation (2.3.14), is:

$$N(t) = \frac{\left(\alpha + \frac{\gamma}{1+\lambda T_D}\right) + b\left(\frac{1-de^{-bt}}{1+de^{-bt}}\right)}{2\beta}$$

$$\text{where} \quad b = \left(\left(\alpha + \frac{\gamma}{1+\lambda T_D}\right)^2 + 4\beta N^* \frac{\gamma\lambda T_D}{1+\lambda T_D}\right)^{1/2} \qquad (2.3.17)$$

$$g = \frac{2\beta N_0 - \alpha - \frac{\gamma}{1+\lambda T_D}}{b}$$

$$d = \frac{1-g}{1+g}$$

This model is illustrated below with the parameters ($N_0 = 19, \alpha = 0.28, \beta = 0.016, \gamma = 0.06$):

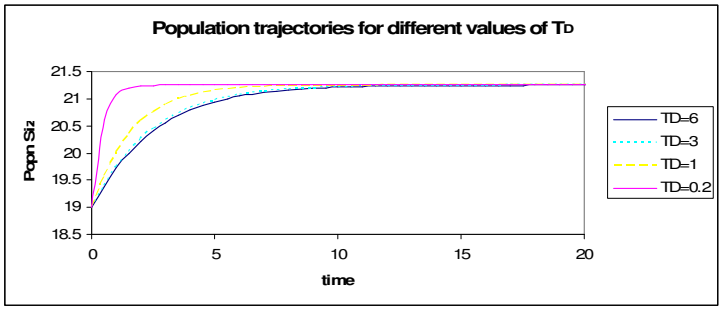


Figure 2.2: Predicted population numbers for a range of time delays

From the above figure, it is clear that the larger the value of the time delay, T_D, the longer it takes the model to reach the equilibrium level of 21.25. This seems to suggest that the more influence the history of the population has on the future population trajectory, the longer it will take the population to reach its equilibrium state.

Kaitala et al. (1996) allowed for the delayed regulation of a population by way of a difference equation:

$$N(t+1) = N(t)F[N(t), N(t-1)]$$
$$\text{where } F[N(t), N(t-1)] = \exp[r + a_1 N(t) + a_2 N(t-1)] \qquad (2.3.18)$$

This model can also decay cyclically to its equilibrium state when subject to random perturbations. The figure below was generated using equation (2.3.18): the initial population size, $N(0)$, has been set at 62, whilst the parameters of the model are set as follows: $r = 0.95$, $a_1 = -0.005$ and $a_2 = -0.01$. Under these parameters, the model predicts a cyclic decay to the equilibrium population size of 63.3.

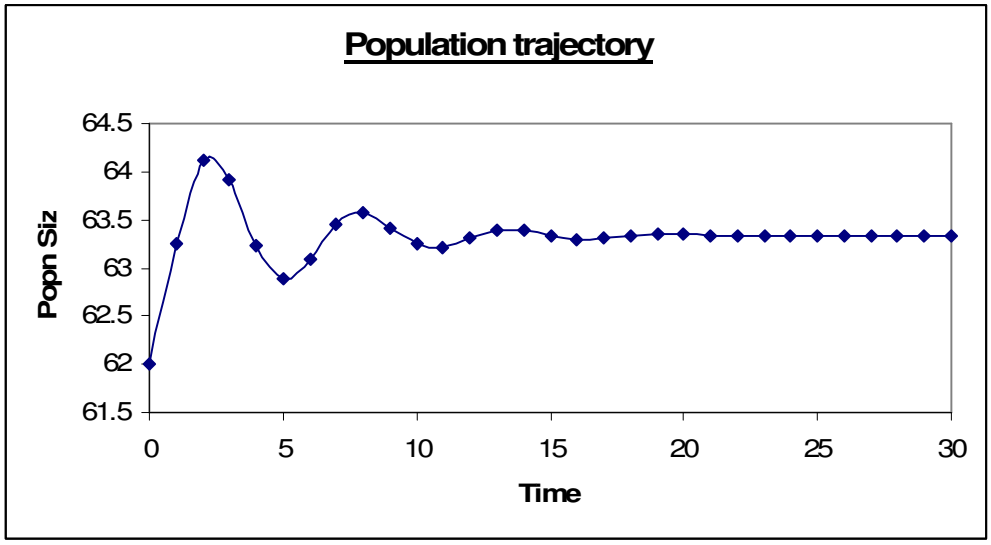


Figure 2.3: A typical trajectory predicted by Equation (2.3.7)

Like the model proposed by Nisbet et al. (equation (2.3.2)), this model is also capable, under certain parameter values, of decaying monotonically to equilibrium.

2.4) Predator-Prey assemblages and the environmental condition

The previous sections have assumed that the future trajectory of the population is completely determined by the history of the population. This section examines two other factors that can be used to predict the population numbers: population numbers for a competing species and the current environmental condition.

A. Predator-Prey assemblages

Consider an ecosystem with two interacting species and denote by $N_1(t)$, $N_2(t)$ the populations of the two species at time t, respectively. If we ignore the delayed response of the populations to N, we can then model the ecosystem by the following two differential equations:

$$\frac{\partial N_1(t)}{\partial t} = \dot{N}_1 = G_1(N_1, N_2) \tag{2.4.1}$$

$$\frac{\partial N_2(t)}{\partial t} = \dot{N}_2 = G_2(N_1, N_2) \tag{2.4.2}$$

Assuming that the ecosystem has a stable equilibrium solution (N_1^*, N_2^*), then we are able to linearize about the steady state.

Consider a displacement from the steady state characterized by:

$$n_1 \equiv N_1 - N_1^*, \quad n_2 \equiv N_2 - N_2^* \tag{2.4.3}$$

A two-dimensional Taylor series expansion of $G_1(N_1^*, N_2^*)$ about the equilibrium state gives us:

$$G_1(N_1, N_2) = G_1(N_1^*, N_2^*) + \left(\frac{\partial G_1}{\partial N_1}\right)^* n_1 + \left(\frac{\partial G_1}{\partial N_2}\right)^* n_2 + O(n^2) \tag{2.4.4}$$

where the star on the partial derivatives indicates that it is evaluated at the equilibrium state of the ecosystem. As in section 2.2, the first term is zero since it is evaluated at the equilibrium state and $O(n^2)$ can be ignored when displacements are sufficiently small. A similar analysis of $G_2(N_1, N_2)$ allows equations (2.4.1) and (2.4.2) to be simplified to:

$$\dot{n}_1 = A_{11} n_1 + A_{12} n_2 \qquad \text{where } A_{ij} = \left(\frac{\partial G_i}{\partial N_j}\right)^* \tag{2.4.5}$$

$$\dot{n}_2 = A_{21} n_1 + A_{22} n_2$$

Nisbet et al. (1982) showed that the equations in (2.4.5) have the solution:

$$\begin{aligned} &n_1 = u_{11} e^{\lambda_1 t} + u_{12} e^{\lambda_2 t}, \quad n_2 = u_{21} e^{\lambda_1 t} + u_{22} e^{\lambda_2 t} \\ &\text{where } \lambda_1 = \tfrac{1}{2}\left[A_{11} + A_{22} + \sqrt{(A_{11} + A_{22})^2 - 4(A_{11}A_{22} - A_{12}A_{21})}\right] \\ &\qquad \lambda_2 = \tfrac{1}{2}\left[A_{11} + A_{22} - \sqrt{(A_{11} + A_{22})^2 - 4(A_{11}A_{22} - A_{12}A_{21})}\right] \end{aligned} \tag{2.4.6}$$

The constants, u_{ij}, can be calculated if one has the initial population sizes. If some of the parameters in equation (2.4.6) are complex, then the above system of equations will have a cyclic decay to equilibrium after a perturbation.

Though each population does not have a delayed response to its current population size, the populations have a delayed response to the other population's size, and this allows for the cyclic decays to occur. For example, if the predator numbers in a predator-prey assemblage were to drop suddenly, the prey would not shift immediately to the modified equilibrium level corresponding to these new conditions. Rather, the prey will move gradually towards its new equilibrium level. The nature of this gradual movement will depend on the model's parameter values. Consider the following model of a host-parasite assemblage:

$$\dot{N}_1 = 0.48N_1 - 0.007N_1^{\,2} - 0.01N_1N_2$$
$$\dot{N}_2 = 0.008N_1N_2 - 0.04N_2$$
where N_1 is the number of hosts and N_2 is the number of parasites

The first equation can be interpreted as follows: the first term on the right hand side of the differential equation is the net per-capita rate at which the host population is increasing; the second term models the effect of crowding on the population (the host population suffers as its habitat becomes more crowded) whilst the third term models the effect of the interaction between the host and the parasite populations (the host population incurs additional deaths due to the parasites). Similarly, the second equation models the parasite population: the first term on the right hand side of the equation indicates that the parasite population increases as the host population increases (as the parasites will have more hosts to feed of) whilst the second term can be interpreted as the effect of crowding on the parasite population. The host's and parasite's delayed reaction to each other's movement causes the decays to equilibrium to be cyclic. If the initial population numbers are $N_1 = 3$ and $N_2 = 8$, the resulting population trajectories for the host and parasite populations can be derived using the above equations:

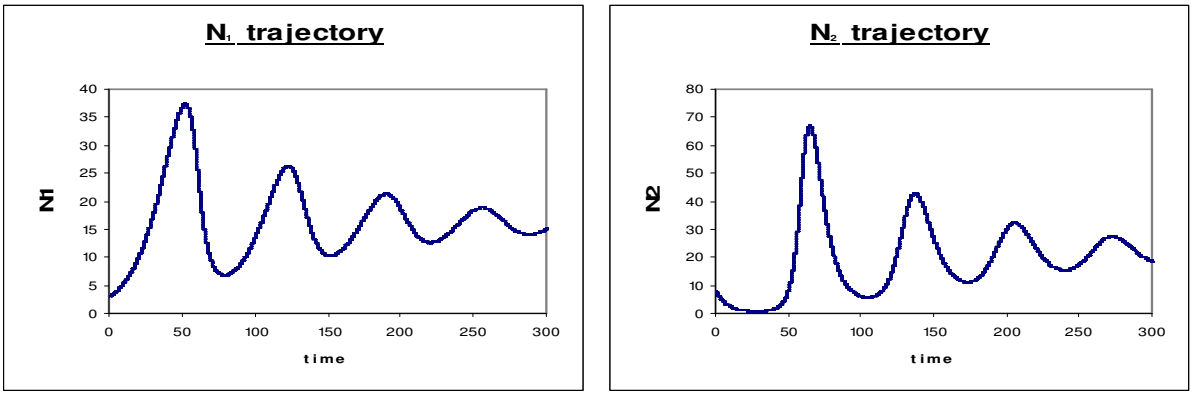


Figure 2.4 Cyclic Decays to equilibrium for a host-parasite assemblage

Kuang et al. (2003) proposed a more general model with k consumer (or predator) species, $N_i(t)$: $i = 1,2,...,k$, competing for a single limited resource, $N_0(t)$:

$$\begin{aligned} \dot{N}_0(t) &= N_0 g(N_0) - \sum_{i=1}^{k} N_i p_i(N_0) \qquad K > N_0(0) > 0, \\ \dot{N}_i(t) &= N_i \left(c_i p_i(N_0) - d_i - m_i N_i - \sum_{j \neq i}^{k} m_{ij} N_j \right) \qquad N_i(0) > 0, i = 1,2,\ldots,k \end{aligned} \tag{2.4.7}$$

Here $g(N_0)$ is the resource per capita growth rate in the absence of predators, K is the carrying capacity for the resource, $p_i(N_0)$ is predator i's functional response to the amount of resources, c_i is the conversion efficiency of predator i, d_i is its constant death rate, m_i is its crowding coefficient and m_{ij} is the response of predator i to crowding from predator j. This model also allows each species to decay cyclically to equilibrium under certain parameter values (See Kuang et al., 2003). Kuang et al. also used the model to infer the conditions that are required for each of the $k+1$ species to persist. For an alternative approach to the problem of species persistence, see Bonneuil (2003).

B. Environmental Condition

So far we have implicitly assumed that the environmental condition, ϕ, remains constant. We now relax this assumption, making ϕ a deterministic, time-dependent quantity. In this case, the transition rates have to be modified to reflect their dependence on the environmental condition. This means:

$$\frac{dN}{dt} = B(N, \phi(t)) - D(N, \phi(t)) \tag{2.4.8}$$

Suppose the average value of ϕ over a long time interval is ϕ^*. Note that if ϕ were to remain constant having a value of ϕ^*, then equation (2.4.8) is structurally equivalent to equation (2.2.1), which has a deterministic equilibrium level N^*. If the equilibrium state is stable, then small fluctuations of ϕ about ϕ^* will result in small displacements of the population from N^*.

Let:

$$n(t) = N(t) - N^*, \qquad f(t) = \phi(t) - \phi^* \tag{2.4.9}$$

be the respective displacements. Then to first order in n and f:

$$\frac{dn}{dt} = \lambda n + \alpha f(t) \qquad \text{where } \lambda = \left[\frac{\partial B}{\partial N} - \frac{\partial D}{\partial N} \right]_{\substack{N=N^* \\ \phi=\phi^*}}, \ \alpha = \left[\frac{\partial B}{\partial \phi} - \frac{\partial D}{\partial \phi} \right]_{\substack{N=N^* \\ \phi=\phi^*}} \tag{2.4.10}$$

The general solution to equation (2.4.10) is of the form:

$$n(t) = '\textit{complementary function}' + '\textit{particular integral}' \qquad (2.4.11)$$

where (i) the complementary function is the solution of equation (2.4.10) when $f(t) = 0$. When $f(t) = 0$, equation (2.4.10) simplifies to equation (2.2.13); which assumes an unchanging environment. Equation (2.2.13) describes the transient dynamics of the population.

(ii) the particular integral is any solution of the differential equation that is independent of the initial conditions. The particular integral models the persistent behaviour of the system (which is determined by $f(t)$), but which is independent of any initial perturbation.

Thus, the solution to equation (2.4.10) consists of a transient part and a persistent part.

We have not, as yet, shown how to solve equation (2.4.10) for periodic functional forms of ϕ. A brief overview of how such a differential equation is to be solved is now given – for a more complete treatment, see Nisbet et al. (1982). Any periodic function ϕ can, by performing a Fourier analysis, be represented as the sum of (a possibly infinite) number of sine and cosine functions; each with their own frequency, ω. The transfer function, $T(\omega)$, characterizes the population's response to each of the sinusoidal driving functions (the driving functions when taken together sum to ϕ). The persistent part of the solution to equation (2.4.10) is the sum, over all the frequencies present in ϕ, of a series of products. The product is the multiplication of the sinusoidal function at a particular frequency with the transfer function, also evaluated at the same frequency. The transfer function is easily obtained by considering the response of the population to a single sinusoidal perturbation. Using this method, we can approximate the future behaviour of any population that is subject to periodic environmental fluctuations. As an example, consider when

$$\frac{dN}{dt} = rN - \frac{rN^2}{\phi(t)} \quad \text{where } \phi(t) = \phi_0(1 + b\cos\omega t) \qquad (2.4.12)$$

Nisbet et al. (1982) obtained the following solution to the above equation, by performing a Fourier analysis (as discussed above) on equation (2.4.12):

$$N(t) = \phi_0\left[1 + \frac{N_0 e^{-rt}}{K_0} + \frac{b}{\sqrt{1+\omega^2/r^2}}\cos(\omega t - \varepsilon)\right] \quad \text{where } \varepsilon = \arctan \omega/r \qquad (2.4.13)$$

One can check that this solution is correct by differentiating it with respect to t and checking that the resulting equation simplifies to Equation (2.4.12). Here, one can see that the effect of the initial population size, N_0, on the population decreases with time. Indeed, in the long term, the population size is independent of the initial population size. Instead, it is a function of the environmental condition; the parameters that define how the environmental condition changes through time and the parameter r (which defines the relationship between the population and the environmental condition).

The above model is an example of how a deterministic model can reveal the interaction between various variables that may be of interest (in this case, the environment is the variable of interest) and the population size. As such, deterministic models are often a valuable tool in understanding the population dynamic. Unfortunately, such models can never be used to model the likelihood of random events that affect a population. We thus now consider a variety of statistical models of the population trajectory.