

STOCHASTIC POPULATION MODELS (SPRING 2011)

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4. FLUCTUATING PARAMETERS IN SINGLE DDE MODELS

4.1. **The general system.** Consider the following population model.

$$(1) \quad \frac{dx}{dt} = f(x, x_\tau, \theta)$$

where $x_\tau(t) = x(t - \tau)$ and where $\theta(t)$ is a small amplitude periodic driver fluctuating about the constant $\bar{\theta}$. Let further

$$(2) \quad 0 = f(\bar{x}, \bar{x}, \bar{\theta})$$

i.e., \bar{x} is an equilibrium solution if $\theta(t) = \bar{\theta}$ for all t . Linearization of the DDE about the point $(x, x_\tau, \theta) = (\bar{x}, \bar{x}, \bar{\theta})$ gives

$$(3) \quad \frac{du}{dt} = au + bu_\tau + c\eta$$

where $u = x - \bar{x}$ and $u_\tau = x_\tau - \bar{x}$ and $\eta = \theta - \bar{\theta}$ and $a = \partial_x f(\bar{x}, \bar{x}, \bar{\theta})$ and $b = \partial_{x_\tau} f(\bar{x}, \bar{x}, \bar{\theta})$ and $c = \partial_\theta f(\bar{x}, \bar{x}, \bar{\theta})$. We assume that the equilibrium \bar{x} is stable if $c = 0$ (i.e., if $\theta(t) = \bar{\theta}$ for all t), the conditions for which have been given in the previous section.

How do the fluctuations in η affect the solution u in the linear DDE? To answer that question we introduce the Fourier integral transform.

4.2. **The Fourier integral transform.** A real or complex function $f(t)$ on $-\infty < t < +\infty$ is absolutely integrable if $\int_{-\infty}^{+\infty} |f(t)| dt$ exists and is finite. The function is piece-wise continuous if it has at most countably many points where it is discontinuous and these points are all isolated.

Suppose f is absolutely integrable and piece-wise continuous. Then the *Fourier transform* of f is defined as the function

$$(4) \quad \tilde{f}(\omega) = \int_{-\infty}^{+\infty} f(t) e^{-i\omega t} dt$$

If \tilde{f} is also absolutely integrable and piece-wise continuous, then, at every point t of continuity,

$$(5) \quad f(t) = \frac{1}{2\pi} \int_{-\infty}^{+\infty} \tilde{f}(\omega) e^{+i\omega t} d\omega$$

which is called the *inverse Fourier transform* of \tilde{f} .

The inverse Fourier transform gives the decomposition of the function $f(t)$ into functions of the form $e^{i\omega t}$ each with a weighing factor $\tilde{f}(\omega)/2\pi$. Since $e^{i\omega t}$ is a periodic function with frequency ω , the amplitude of the ω -frequency component in the function $f(t)$ is given by $|\tilde{f}(\omega)|/2\pi$. This is a useful observation, because we are interested in how a population model transforms the amplitudes of the various frequency components in the driver.

Here are some useful properties of the Fourier transform:

- (a) The Fourier transform and the inverse Fourier transform are linear operators (i.e., the transform of a linear combination of functions is equal to the linear combination of the transforms of the same functions).
- (b) $\tilde{\tilde{f}}(t) = 2\pi f(-t)$
- (c) $\widetilde{\left(\frac{d}{dt}f\right)}(\omega) = i\omega\tilde{f}(\omega)$
- (d) $\frac{d}{d\omega}\tilde{f}(\omega) = -i\widetilde{(tf)}(\omega)$
- (e) $\tilde{f}_\tau(\omega) = e^{-i\omega\tau}\tilde{f}(\omega)$ where $f_\tau(t) := f(t - \tau)$
- (f) $\widetilde{(f * h)}(\omega) = \tilde{f}(\omega)\tilde{h}(\omega)$ where $(f * h)(t) := \int_{-\infty}^{+\infty} f(\tau)h(t - \tau)d\tau$
- (g) $\widetilde{(fh)}(\omega) = (\tilde{f} * \tilde{h})(\omega)$
- (h) $\int_{-\infty}^{+\infty} f(t)\tilde{h}(t)dt = \int_{-\infty}^{+\infty} \tilde{f}(t)h(t)dt$

The proofs are left as an exercise.

4.3. The Dirac delta distribution. The Fourier transform requires absolute integrability. This excludes such functions as t^n , $\cos(\omega_0 t)$, $e^{i\omega_0 t}$ and other common functions. To remedy this, we introduce the *Dirac delta distribution*. The Dirac delta distribution is a probability distribution where all probability mass is concentrated at zero. If we formally denote the probability “density” of the Dirac delta distribution by $\delta(t)$, then

$$(6) \quad \int_{-\infty}^{+\infty} \delta(t)dt = 1$$

and

$$(7) \quad \int_{-\infty}^{+\infty} \delta(t)f(t)dt = \mathcal{E}\{f(t)\} = f(0)$$

and, in particular,

$$(8) \quad \tilde{\delta}(\omega) = \int_{-\infty}^{+\infty} \delta(t)e^{-i\omega t}dt = \mathcal{E}\{e^{-i\omega t}\} = 1$$

Using the above together with property (b) of the list of properties of the Fourier transform in the previous subsection, we find that

$$(9) \quad \tilde{1} = \tilde{\delta}(t) = 2\pi\delta(-t) = 2\pi\delta(t)$$

We thus find that the Fourier transform of a constant function (even though a constant function that is not identical to zero is not absolutely integrable) exists provided we accept the Dirac delta distribution as a legitimate mathematical object.

Here are some more functions that are not absolutely integrable and yet have a Fourier transform:

$$(a) \quad \widetilde{(t^n)}(\omega) = 2(n+1)!\pi\delta(\omega)/(i\omega)^n \quad \text{for } n = 0, 1, \dots$$

$$(b) \quad \widetilde{e^{i\omega_0 t}}(\omega) = 2\pi\delta(\omega - \omega_0)$$

$$(c) \quad \widetilde{\cos(\omega_0 t)} = \pi\delta(\omega - \omega_0) + \pi\delta(\omega + \omega_0)$$

The proofs are left as an exercise.

4.4. The transfer function. We can solve the linear DDE (3) using the Fourier transform (4) and its inverse (5): taking Fourier transforms on both sides of the linear DDE (3) gives

$$(10) \quad i\omega\tilde{u}(\omega) = a\tilde{u}(\omega) + be^{-i\omega\tau}\tilde{u}(\omega) + c\tilde{\eta}(\omega)$$

which can be solved for $\tilde{u}(\omega)$:

$$(11) \quad \tilde{u}(\omega) = \frac{c}{i\omega - a - be^{-i\omega\tau}} \tilde{\eta}(\omega)$$

Taking the inverse Fourier transform, we get an explicit solution of the linear DDE:

$$(12) \quad u(t) = \frac{1}{2\pi} \int_{-\infty}^{+\infty} \frac{ce^{i\omega t}\tilde{\eta}(\omega)}{i\omega - a - be^{-i\omega\tau}} d\omega$$

How useful this explicit solution is I do not know. Actually, much more useful is equation (11), which we rewrite as

$$(13) \quad \tilde{u}(\omega) = T(\omega)\tilde{\eta}(\omega)$$

where

$$(14) \quad T(\omega) = \frac{c}{i\omega - a - be^{-i\omega\tau}}$$

is the transfer function.

Remember from section (4.2) that $|\tilde{\eta}(\omega)|/2\pi$ is the amplitude of the ω -frequency component in the function $\tilde{\eta}$, and $|\tilde{u}(\omega)|/2\pi$ is the amplitude of the ω -frequency component in the function \tilde{u} . So, the amplification factor, or gain, for the frequency ω is given by $|\tilde{u}(\omega)|/|\tilde{\eta}(\omega)| = |T(\omega)|$. Likewise, the phase-shift is given by $\arg T(\omega)$. (Notice that these results are consistent with what we found for the ODEs in Section 2.2.)

We now shall apply the above to a number of examples.

4.5. **Example.** This is a continuation of the example if Section 3.1, Equation (6):

$$(15) \quad \frac{dx}{dt} = p\beta x_\tau - \delta x - \frac{\gamma}{2}x^2$$

where β is the birth rate, γ the contest rate, δ the mortality rate of adults, and τ the fixed developmental delay. The parameter p is the survival probability of juveniles, i.e., the probability that a newborn survives till age τ and becomes an adult. With a constant juvenile death rate α , we would have $p = e^{-\alpha\tau}$.

If the parameters are not constants but vary in time, then we must be very careful about those parameters that are associated with some event in the past. For example, the birth rate β in the above equation becomes the birth rate at time $t - \tau$ and not at time t , i.e., $\beta_\tau(t) := \beta(t - \tau)$ and not $\beta(t)$. Likewise, the survival probability p becomes the probability of surviving the juvenile stage from time $t - \tau$ till time t , i.e., $p(t) = \exp\{-\int_{t-\tau}^t \alpha(s)ds\}$, which we can write as $p(t) = e^{-\alpha_\psi(t)\tau}$ where ψ is the uniform distribution over the interval $(0, \tau)$ and

$$(16) \quad \alpha_\psi(t) = \int_0^\infty \alpha(t-s)\psi(s)ds$$

is the average juvenile mortality rate between $t - \tau$ and t . The parameters δ and γ act instantaneously and therefore can be treated in a straightforward way. Rewriting the above model with varying parameters thus gives

$$(17) \quad \frac{dx(t)}{dt} = e^{-\alpha_\psi(t)\tau}\beta_\tau(t)x_\tau(t) - \delta(t)x(t) - \frac{\gamma(t)}{2}x(t)^2$$

We shall vary only one parameter in turn.

4.6. **Varying the adult mortality rate.** Varying the adult mortality rate δ in equation (17) while keeping the other parameters constant gives

$$(18) \quad \frac{dx(t)}{dt} = \beta e^{-\alpha\tau}x_\tau(t) - \delta(t)x(t) - \frac{\gamma}{2}x(t)^2$$

For constant $\delta(t) = \bar{\delta}$, the equilibrium would be

$$(19) \quad \bar{x} = \frac{2}{\gamma}(\beta e^{-\alpha\tau} - \bar{\delta})$$

Linearization at $(x, x_\tau, \delta) = (\bar{x}, \bar{x}, \bar{\delta})$ gives

$$(20) \quad \frac{du}{dt} = -(\bar{\delta} + \gamma\bar{x})u + \beta e^{-\alpha\tau}u_\tau - \bar{x}\eta$$

where $u = x - \bar{x}$ and $u_\tau = x_\tau - \bar{x}$ and $\eta = \delta - \bar{\delta}$. Taking Fourier transforms on both sides gives

$$(21) \quad i\omega\tilde{u}(\omega) = -(\bar{\delta} + \gamma\bar{x})\tilde{u}(\omega) + \beta e^{-\alpha\tau - i\omega\tau}\tilde{u}(\omega) - \bar{x}\tilde{\eta}(\omega)$$

Solving for \tilde{u} gives

$$(22) \quad \tilde{u}(\omega) = \frac{-\bar{x}}{i\omega + \bar{\delta} + \gamma\bar{x} - \beta e^{-\alpha\tau - i\omega\tau}}\tilde{\eta}(\omega)$$

The transfer function thus is

$$(23) \quad T(\omega) = \frac{-\bar{x}}{i\omega + \bar{\delta} + \gamma\bar{x} - \beta e^{-\alpha\tau - i\omega\tau}}$$

The following figures give the main filter characteristics of the model with respect to fluctuations in the parameter δ .

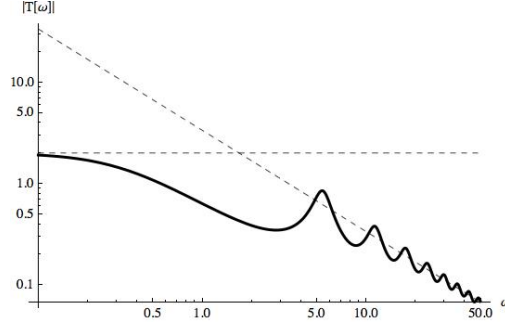


FIGURE 1. Gain vs. frequency for fluctuations in δ .

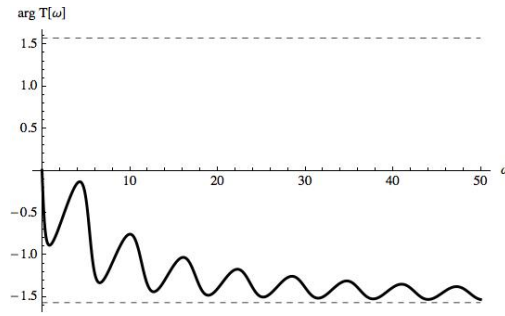


FIGURE 2. Phase-shift vs. frequency for fluctuations in δ .

4.7. Varying the birth rate. Varying the birth rate β in equation (17) while keeping the other parameters constant gives

$$(24) \quad \frac{dx(t)}{dt} = e^{-\alpha\tau} \beta_\tau(t) x_\tau(t) - \delta x(t) - \frac{\gamma}{2} x(t)^2$$

For constant $\beta(t) = \bar{\beta}$, the equilibrium would be

$$(25) \quad \bar{x} = \frac{2}{\gamma} (\bar{\beta} e^{-\alpha\tau} - \delta)$$

Linearization at $(x, x_\tau, \beta) = (\bar{x}, \bar{x}, \bar{\beta})$ gives

$$(26) \quad \frac{du}{dt} = -(\delta + \gamma\bar{x})u + \bar{\beta} e^{-\alpha\tau} u_\tau + \bar{x} e^{-\alpha\tau} \eta_\tau$$

where $u = x - \bar{x}$ and $u_\tau = x_\tau - \bar{x}$ and $\eta_\tau = \beta_\tau - \bar{\beta}$. Taking Fourier transforms on both sides gives

$$(27) \quad i\omega \tilde{u}(\omega) = -(\delta + \gamma\bar{x})\tilde{u}(\omega) + \bar{\beta} e^{-\alpha\tau - i\omega\tau} \tilde{u}(\omega) + \bar{x} e^{-\alpha\tau - i\omega\tau} \tilde{\eta}(\omega)$$

Solving for \tilde{u} gives

$$(28) \quad \tilde{u}(\omega) = \frac{\bar{x}e^{-\alpha\tau-i\omega\tau}}{i\omega + \delta + \gamma\bar{x} - \bar{\beta}e^{-\alpha\tau-i\omega\tau}}\tilde{\eta}(\omega)$$

The transfer function thus is

$$(29) \quad T(\omega) = \frac{\bar{x}e^{-\alpha\tau-i\omega\tau}}{i\omega + \delta + \gamma\bar{x} - \bar{\beta}e^{-\alpha\tau-i\omega\tau}}$$

The following figures give the main filter characteristics of the model with respect to fluctuations in the parameter β .

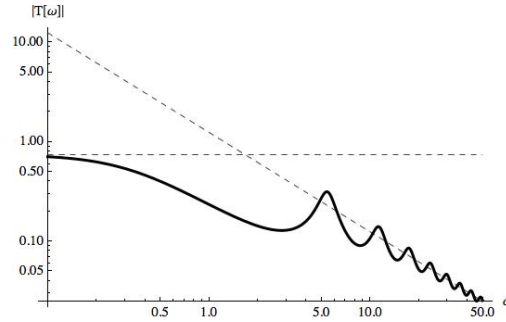


FIGURE 3. Gain vs. frequency for fluctuations in β .

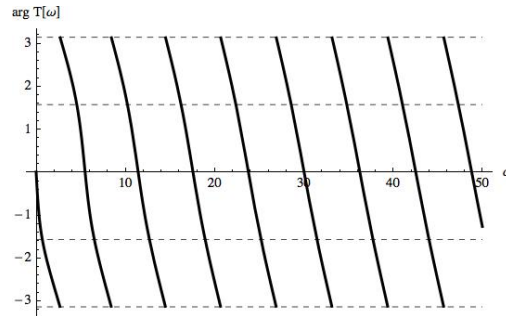


FIGURE 4. Phase-shift vs. frequency for fluctuations in β .

4.8. Varying the juvenile death rate. Varying the juvenile death rate α in equation (17) while keeping the other parameters constant gives

$$(30) \quad \frac{dx(t)}{dt} = \beta e^{-\alpha\psi(t)\tau}x_\tau(t) - \delta x(t) - \frac{\gamma}{2}x(t)^2$$

For constant $\alpha(t) = \bar{\alpha}$, the equilibrium would be

$$(31) \quad \bar{x} = \frac{2}{\gamma}(\beta e^{-\bar{\alpha}\tau} - \delta)$$

Linearization at $(x, x_\tau, \alpha) = (\bar{x}, \bar{x}, \bar{\alpha})$ gives

$$(32) \quad \frac{du}{dt} = -(\delta + \gamma\bar{x})u + \beta e^{-\bar{\alpha}\tau}u_\tau - \tau\bar{x}\beta e^{-\bar{\alpha}\tau}\eta_\psi$$

where $u = x - \bar{x}$ and $u_\tau = x_\tau - \bar{x}$ and $\eta_\psi = \alpha_\psi - \bar{\alpha}$. To calculate the Fourier transform of η_ψ , notice that $\eta_\psi = \eta * \phi$, and so we can use property (f) from Section 4.2. The only thing we have to know then is the Fourier transform of ψ , which is directly calculated from the definition (4) and turns out to be

$$(33) \quad \tilde{\psi}(\omega) = \frac{1}{\tau} \int_0^\tau e^{-i\omega t} dt = \frac{1 - e^{-i\omega\tau}}{i\omega\tau}$$

Taking Fourier transforms on both sides of Equation (32) gives

$$(34) \quad i\omega\tilde{u}(\omega) = -(\delta + \gamma\bar{x})\tilde{u}(\omega) + \beta e^{-\bar{\alpha}\tau - i\omega\tau}\tilde{u}(\omega) - \frac{\tau\bar{x}\beta e^{-\bar{\alpha}\tau}(1 - e^{-i\omega\tau})}{i\omega\tau}\tilde{\eta}(\omega)$$

Solving for \tilde{u} gives

$$(35) \quad \tilde{u}(\omega) = \frac{-\tau\bar{x}\beta e^{-\bar{\alpha}\tau}(1 - e^{-i\omega\tau})}{(i\omega + \delta + \gamma\bar{x} - \beta e^{-\bar{\alpha}\tau - i\omega\tau})(i\omega\tau)}\tilde{\eta}(\omega)$$

The transfer function thus is

$$(36) \quad T(\omega) = \frac{-\tau\bar{x}\beta e^{-\bar{\alpha}\tau}(1 - e^{-i\omega\tau})}{(i\omega + \delta + \gamma\bar{x} - \beta e^{-\bar{\alpha}\tau - i\omega\tau})(i\omega\tau)}$$

The following figures give the main filter characteristics of the model with respect to fluctuations in the parameter α .

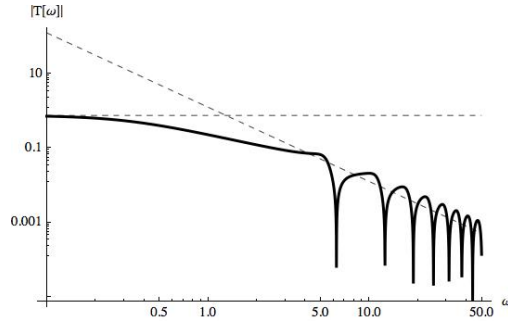


FIGURE 5. Gain vs. frequency for fluctuations in α .

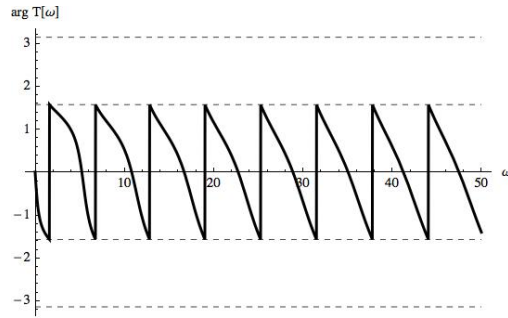


FIGURE 6. Phase-shift vs. frequency for fluctuations in α .