STOCHASTIC POPULATION MODELS (SPRING 2011)

STEFAN GERITZ
DEPARTMENT OF MATHEMATICS AND STATISTICS
UNIVERSITY OF HELSINKI

7. Population models with stochastic parameters

7.1. **Motivating example.** Consider the population model

$$\frac{dX}{dt} = f(X, \theta) \tag{1}$$

where θ is a stationary stochastic process with mean $\bar{\theta}$. Let $\bar{X}$ be a positive equilibrium for constant $\theta = \bar{\theta}$, i.e.,

$$f(\bar{X}, \bar{\theta}) = 0 \tag{2}$$

Local linearization around the point $(\bar{X}, \bar{\theta})$ gives

$$\frac{du}{dt} - au = b\eta \tag{3}$$

where $a = \partial_X f(\bar{X}, \bar{\theta})$ and $b = \partial_\theta f(\bar{X}, \bar{\theta})$ and $u = X - \bar{X}$ and $\eta = \theta - \bar{\theta}$. For deterministic stability of $\bar{X}$ we assume that $a < 0$.

Calculating the auto-covariances on both sides of the above equation gives

$$-C_u''(\tau) + a^2 C_u(\tau) = b^2 C_\eta(\tau) \tag{4}$$

Taking Fourier transforms gives

$$\omega^2 S_u(\omega) + a^2 S_u(\omega) = b^2 S_\eta(\omega) \tag{5}$$

from which we get

$$\begin{cases} S_u(\omega) = |T(\omega)|^2 S_\eta(\omega) \\ T(\omega) = \frac{b}{i\omega - a} \end{cases} \tag{6}$$

where $T(\omega)$ is our old friend the transfer function from Section 2.1 equation (8). This raises the question whether it is always so that the spectral density of the output of a linear system is equal to the spectral density of the input signal times the modulus of the transfer function squared. i.e., $S_u(\omega) = |T(\omega)|^2 S_\eta(\omega)$ irrespective of the particulars of the model?

7.2. **Ergodic processes.** A stationary process $\{X(t)\}$ is *ergodic* if time-averages equal ensemble averages, i.e., if

$$\mathcal{E}\{f(X(t))\} = \lim_{T\to\infty} \frac{1}{2T} \int_{-T}^{T} f(x(t'))dt' \tag{7}$$

for every integrable function f and every single sample path (i.e., realization) $\{x(t)\}$ of the process $\{X(t)\}$.

If a stationary process is ergodic, then a single realization of the process over infinite time contains all information about the distribution of the process at any particular fixed time. For convenience we denote the time-average by $\langle\cdot\rangle$, and hence a stationary stochastic process $\{X(t)\}$ is ergodic if

$$\mathcal{E}\big\{f\big(X(t)\big)\big\} = \big\langle f(x(t))\big\rangle \tag{8}$$

for every integrable function f and every realization $x(t)$.

In particular, if $\{X(t)\}$ is ergodic, then for the mean we have

$$\overline{X} = \big\langle x(t)\big\rangle \tag{9}$$

and for the auto-covariance

$$C(\tau) = \big\langle (x(t+\tau) - \overline{X})(x(t) - \overline{X})\big\rangle \tag{10}$$

A sufficient condition for a stationary process $\{X(t)\}$ to be ergodic is (**a**) that its auto covariance $C_X(t) \to 0$ as $t \to \infty$ and (**b**) that the process is irreducible, i.e., for every starting point x_0 and every non-empty open set A there is $t > 0$ such that $\text{Prob}\{X(t) \in A \,|\, X(0) = x_0\} > 0$.

7.3. **The Wiener-Khinchin theorem.** Suppose $\{X(t)\}$ is ergodic with auto-covariance $C(\tau)$ and spectral density $S(\omega)$ and define the random variable

$$S_T(\omega) := \frac{1}{2T} \left| \int_{-T}^{T} \big(X(t) - \overline{X}\big)e^{-i\omega t}dt \right|^2 \tag{11}$$

Then

$$S(\omega) = \lim_{T\to\infty} \mathcal{E}\big\{S_T(\omega)\big\} \tag{12}$$

whenever $\tau C(\tau)$ is absolutely integrable.

(The Wiener-Khinchin theorem provides us with an interpretation of the spectral density: the spectral density gives the relative contributions of different angular frequencies in the sample path $x(t)$.)

Proof:

Writing the square in (11) as a double integral, we have

$$\begin{aligned} S_T(\omega) &= \tfrac{1}{2T} \textstyle\int_{-T}^{T} \big(X(t_1) - \overline{X}\big)e^{-i\omega t_1}dt_1 \int_{-T}^{T} \big(X(t_2) - \overline{X}\big)e^{+i\omega t_2}dt_2 \\ &= \tfrac{1}{2T} \textstyle\int_{-T}^{T}\int_{-T}^{T} \big(X(t_1) - \overline{X}\big)\big(X(t_2) - \overline{X}\big)e^{-i\omega(t_1-t_2)}dt_1dt_2 \end{aligned} \tag{13}$$

Taking expectations gives

$$\mathcal{E}\{S_T(\omega)\} = \frac{1}{2T}\int_{-T}^{T}\int_{-T}^{T} C(t_1 - t_2)e^{-i\omega(t_1-t_2)}dt_1 dt_2 \tag{14}$$

A simple exercise in calculus shows that for any integrable function f we have

$$\int_{-T}^{T}\int_{-T}^{T} f(t_1 - t_2)dt_1 dt_2 = \int_{-2T}^{2T}(2T - |\tau|)f(\tau)d\tau \tag{15}$$

and so, with $f(t) = C(t)e^{-i\omega t}$, we get

$$\begin{aligned} \mathcal{E}\{S_T(\omega)\} &= \tfrac{1}{2T}\textstyle\int_{-2T}^{2T}(2T - |\tau|)C(\tau)e^{-i\omega\tau}d\tau \\ &= \textstyle\int_{-2T}^{2T} C(\tau)e^{-i\omega\tau}d\tau - \tfrac{1}{2T}\int_{-2T}^{2T}|\tau|C(\tau)e^{-i\omega\tau}d\tau \end{aligned} \tag{16}$$

If $\tau C(\tau)$ is absolutely integrable, then the last term vanishes as $T \to \infty$. The first term, however, converges to the Fourier transform of the auto-covariance, i.e., to the spectral density $S(\omega)$. This completes the proof.

7.4. **A general property of population models with ergodic parameters.** Let $T(\omega)$ be the transfer function of an arbitrary (linearized) population model, i.e.,

$$\tilde{u}(\omega) = T(\omega)\tilde{\eta}(\omega) \tag{17}$$

where $u = x - \bar{x}$ and $\eta = \theta - \bar{\theta}$ are small deviations of, respectively, the population density from the deterministic equilibrium and a randomly fluctuating parameter from its time-average. Then

$$S_X(\omega) = \left|T(\omega)\right|^2 S_\theta(\omega) \tag{18}$$

Proof:

From the Wiener-Khinchin theorem we have

$$\begin{aligned} S_X(\omega) &= \lim_{T\to\infty}\tfrac{1}{2T}\mathcal{E}\left\{\left|\textstyle\int_{-T}^{T} u(t)e^{-i\omega t}dt\right|^2\right\} \\ &= \lim_{T\to\infty}\tfrac{1}{2T}\mathcal{E}\left\{|\tilde{u}(\omega) + \mathrm{o}(1)|^2\right\} \\ &= \lim_{T\to\infty}\tfrac{1}{2T}\mathcal{E}\left\{|T(\omega)\tilde{\eta}(\omega) + \mathrm{o}(1)|^2\right\} \\ &= \left|T(\omega)\right|^2 \lim_{T\to\infty}\tfrac{1}{2T}\mathcal{E}\left\{|\tilde{\eta}(\omega) + \mathrm{o}(1)|^2\right\} \\ &= \left|T(\omega)\right|^2 \lim_{T\to\infty}\tfrac{1}{2T}\mathcal{E}\left\{\left|\textstyle\int_{-T}^{T}\eta(t)dt + \mathrm{o}(1)\right|^2\right\} \\ &= \left|T(\omega)\right|^2 S_\theta(\omega) \end{aligned} \tag{19}$$

7.5. **Example.** Consider the model of section 4.5 with a fluctuating birth rate, i.e.,

$$\frac{dX(t)}{dt} = e^{-\alpha\tau}\beta_\tau(t)X_\tau(t) - \delta X(t) - \frac{1}{2}\gamma X(t)^2 \tag{20}$$

In section 4.7 we calculated the transfer function as

$$T(\omega) = \frac{\bar{X}e^{-\alpha\tau - i\omega\tau}}{i\omega + \delta + \gamma\bar{X} - \bar{\beta}e^{-\alpha\tau - i\omega\tau}} \tag{21}$$

where

$$\bar{X} = 2\big(e^{-\alpha\tau}\bar{\beta} - \delta\big)/\gamma \tag{22}$$

is the equilibrium population density for a constant birth rate $\bar{\beta}$.

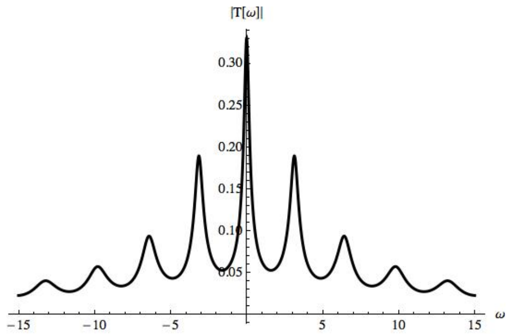

FIGURE 1. Modulus of the transfer function or "gain" for $\alpha = 1$, $\bar{\beta} = 20$, $\gamma = 1$, $\delta = 2$ and $\tau = 1.8$.

Suppose the birth rate $\beta(t)$ is given by the stochastic process

$$\beta(t) = \bar{\beta}e^{\zeta(t)} \tag{23}$$

where $\{\zeta(t)\}$ is the stationary Ornstein-Uhlenbeck process from section 6.2 (with parameters $a = 10$ and $b = 0.5$). The following figure gives a sample path of the population process $\{X(t)\}$ obtained by numerical integration of the differential equation (20).

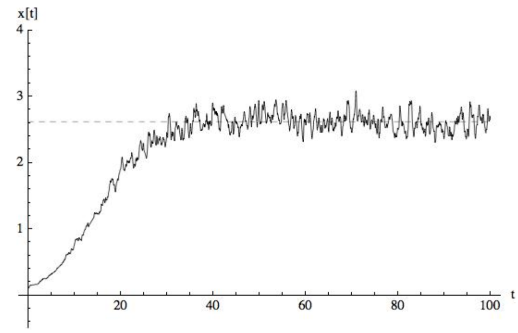

FIGURE 2. Sample path of $\{X(t)\}$ for $\alpha = 1$, $\bar{\beta} = 20$, $\gamma = 1$, $\delta = 2$ and $\tau = 1.8$. The dashed line indicates the value of $\bar{X}$.

The spectral density $S_\zeta(\omega)$ of the stationary Ornstein-Uhlenbeck process was calculated in section 6.4. Moreover, from section 6.7 we know that if the amplitude of the fluctuations in ζ is not too large, then the spectral density for $\beta(t)$ is approximately

$$S_\beta(\omega) = \bar{\beta}^2 S_\zeta(\omega) \tag{24}$$

From the result in equation (18) in section 7.4 we thus find

$$S_X(\omega) = \bar{\beta}^2 \big|T(\omega)\big|^2 S_\zeta(\omega) \tag{25}$$

and so

$$C_X(t) = \frac{\bar{\beta}^2}{2\pi} \int_{-\infty}^{\infty} \big|T(\omega)\big|^2 S_\zeta(\omega) e^{i\omega t} d\omega \tag{26}$$

which is best calculated numerically

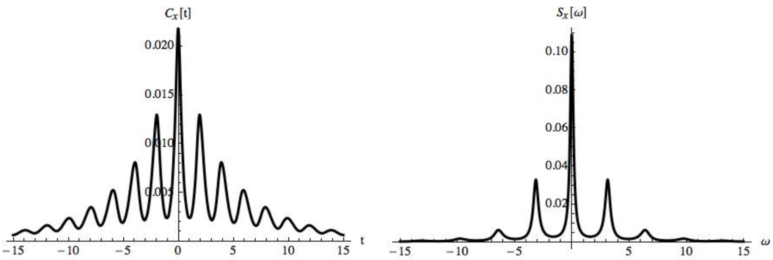

FIGURE 3. The auto-covariance and spectral density of the population process $\{X(t)\}$ for $\alpha = 1$, $\bar{\beta} = 20$, $\gamma = 1$, $\delta = 2$ and $\tau = 1.8$.

The spectral density shows a strong resonance peak at $\omega = \pm 3$. This is solely due to the transfer function, because there are no dominant peaks in the spectrum of the Ornstein-Uhlenbeck process aside from $\omega = 0$. Although the presence of a periodic component in the sample path in one of the above figures is not so obvious, we can exploit the ergodicity of the population process, and calculate (or approximate) the auto-covariance and spectral density also directly from the sample path.

Given the sample path $\{x(t)\}$ for $t \in (t_1, t_2)$, the auto-covariance can be approximated by the time-average

$$C_X(\tau) \approx \big\langle (x(t+\tau) - \bar{X})(x(t) - \bar{X}) \big\rangle \tag{27}$$

and using the Wiener-Khinchin theorem, the spectral density by the time-average

$$S_X(\tau) \approx (t_2 - t_1) \big| \big\langle (x(t) - \bar{X}) e^{-i\omega t} \big\rangle \big|^2 \tag{28}$$

as illustrated in the following figure. Note that while these approximations are calculated from a single sample path of the original *nonlinear* model, the results are very similar to the auto-covariance and spectral density calculated analytically from a linearization of the model assuming small amplitude fluctuations. The linearization thus gives fairly robust results.

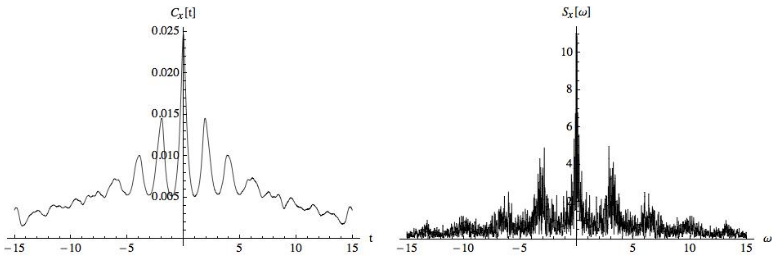

FIGURE 4. The auto-covariance and spectral density estimated from the sample path $\{x(t)\}$.