7. Population models with stochastic parameters

7.1. Motivating example. Consider the population model

\begin{equation}
\frac{dX}{dt} = f(X, \theta)
\end{equation}

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

\begin{equation}
f(\bar{X}, \bar{\theta}) = 0
\end{equation}

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

\begin{equation}
\frac{du}{dt} = au + b\eta
\end{equation}

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 \( a < 0 \).

(Note that, because of non-linearities, \( \bar{X} \) is typically not the mean of the stationary process generated by equation (1). However, \( \bar{X} \) is the mean of \( X(t) \) in the stationary process generated by the linear equation (3). Indeed, if \( \{u(t)\} \) is stationary, then \( 0 = \frac{1}{\Delta t} \mathcal{E}\{u\} = \mathcal{E}\{\frac{1}{\Delta t} u\} = \mathcal{E}\{au + b\eta\} = a\mathcal{E}\{u\} \) because \( \mathcal{E}\{\eta\} = \mathcal{E}\{\theta\} - \bar{\theta} = 0 \). Hence, \( 0 = \mathcal{E}\{u\} = \mathcal{E}\{X\} - \bar{X} \) and so \( \mathcal{E}\{X\} = \bar{X} \).)

Calculating the auto-covariances from the linear equation (3) we get

\begin{equation}
-C_u''(\tau) + a^2 C_u(\tau) = b^2 C_{\eta}(\tau)
\end{equation}

Taking Fourier transforms gives

\begin{equation}
\omega^2 S_u(\omega) + a^2 S_u(\omega) = b^2 S_\eta(\omega)
\end{equation}

from which we get

\begin{align}
S_u(\omega) &= |T(\omega)|^2 S_\eta(\omega) \\
T(\omega) &= \frac{b}{\omega - a}
\end{align}

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

\[
E \{ f(X(t)) \} = \lim_{T\to\infty} \frac{1}{2T} \int_{-T}^{T} f(x(t')) dt'
\]

for every integrable function \( f \) and almost 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

\[
E \{ f(X(t)) \} = \langle f(x(t)) \rangle
\]

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

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

\[
\bar{X} = \langle x(t) \rangle
\]

and for the auto-covariance

\[
C(\tau) = \langle (x(t + \tau) - \bar{X})(x(t) - \bar{X}) \rangle
\]

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 \( \text{Prob}\{X(t) \in A \mid X(0) = x_0\} > 0 \).

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

\[
S_T(\omega) := \frac{1}{2T} \left| \int_{-T}^{T} (X(t) - \bar{X}) e^{-i\omega t} dt \right|^2
\]

Then

\[
S(\omega) = \lim_{T\to\infty} E\{S_T(\omega)\}
\]

whenever \( |\tau|C(\tau) \) is 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

\[ S_T(\omega) = \frac{1}{2T} \int_{-T}^{T} (X(t_1) - \overline{X}) e^{-i\omega t_1} dt_1 \int_{-T}^{T} (X(t_2) - \overline{X}) e^{+i\omega t_2} dt_2 \]

or

\[ S_T(\omega) = \frac{1}{2T} \int_{-T}^{T} (X(t_1) - \overline{X}) (X(t_2) - \overline{X}) e^{-i\omega (t_1 - t_2)} dt_1 dt_2 \]

Taking expectations gives

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

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

\[ \int_{-T}^{T} \int_{-T}^{T} f(t_1 - t_2) dt_1 dt_2 = \int_{-2T}^{2T} (2T - |\tau|) f(\tau) d\tau \]

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

\[ \mathcal{E}\{S_T(\omega)\} = \frac{1}{2T} \int_{-2T}^{2T} (2T - |\tau|) C(\tau) e^{-i\omega \tau} d\tau \]

or

\[ \mathcal{E}\{S_T(\omega)\} = \int_{-2T}^{2T} C(\tau) e^{-i\omega \tau} d\tau - \frac{1}{2T} \int_{-2T}^{2T} |\tau| C(\tau) e^{-i\omega \tau} d\tau \]

If \( |\tau| C(\tau) \) is 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.,

\[ \tilde{u}(\omega) = T(\omega) \tilde{\eta}(\omega) \]

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

\[ S_\chi(\omega) = |T(\omega)|^2 S_\theta(\omega) \]

Proof:
From the Wiener-Khinchin theorem we have
\[
S_X(\omega) = \lim_{T \to \infty} \frac{1}{2\pi} \mathbb{E} \left\{ \left| \int_{-T}^{T} u(t)e^{-i\omega t} dt \right|^2 \right\}
\]
\[
= \lim_{T \to \infty} \frac{1}{2\pi} \mathbb{E} \left\{ |\tilde{u}(\omega) + o(1)|^2 \right\}
\]
\[
= \lim_{T \to \infty} \frac{1}{2\pi} \mathbb{E} \left\{ |T(\omega)\tilde{\eta}(\omega) + o(1)|^2 \right\}
\]
\[
= |T(\omega)|^2 \lim_{T \to \infty} \frac{1}{2\pi} \mathbb{E} \left\{ |\tilde{\eta}(\omega) + o(1)|^2 \right\}
\]
\[
= |T(\omega)|^2 \lim_{T \to \infty} \frac{1}{2\pi} \mathbb{E} \left\{ |\int_{-T}^{T} \eta(t)e^{-i\omega t} dt + o(1)|^2 \right\}
\]
\[
= |T(\omega)|^2 S_\theta(\omega)
\]

7.5. Example. Consider the model of section 4.5 with a fluctuating birth rate, i.e.,
\[
\frac{dX(t)}{dt} = e^{-\alpha \tau} \beta_t(t)X_\tau(t) - \delta X(t) - \frac{1}{2} \gamma X(t)^2
\]
In section 4.7 we calculated the transfer function as
\[
T(\omega) = \bar{X} e^{-\alpha \tau - i\omega \tau} (i\omega + \delta + \gamma \bar{X} - \beta e^{-\alpha \tau - i\omega \tau})
\]
where \(\bar{\beta}\) is the average birth rate and
\[
\bar{X} = 2(e^{-\alpha \tau} \bar{\beta} - \delta) / \gamma
\]
is the deterministic equilibrium of the population density if the birth rate were a constant \(\bar{\beta}\). We have seen in section 3.3 that the deterministic equilibrium is stable whenever it exists. Suppose the birth rate \(\beta(t)\) is given by the stochastic process
\[
\beta(t) = \beta_0 e^{\zeta(t)}
\]
where \(\{\zeta(t)\}\) is the stationary Ornstein-Uhlenbeck generated by the linear SDE
\[
d\zeta + a\zeta dt = bdW
\]
for \(a, b > 0\) (see section 6.2). The average birth rate \(\bar{\beta}\) then can be approximated as
\[
\bar{\beta} \approx \beta_0 \left(1 + \frac{b^2}{4a}\right)
\]
and the spectral density as
\[
S_\beta \approx \frac{\beta_0^2 b^2}{\omega^2 + a^2}
\]
provided $b^2/2a$ (i.e., the variance of $\zeta$) is not too large (see section 6.7). Applying equation (18) in the previous section, we thus have

\begin{equation}
S_X(\omega) = |T(\omega)|^2 S_\beta(\omega)
\end{equation}

\begin{equation}
\approx |T(\omega)|^2 \frac{\beta_0^2 b^2}{\omega^2 + \alpha^2}
\end{equation}

which is plotted in the figure below.

\begin{figure}
\centering
\includegraphics[width=\textwidth]{figure1.png}
\caption{The auto-covariance and spectral density of the population process $\{X(t)\}$ for $\alpha = 1$, $\beta = 20$, $\gamma = 1$, $\delta = 2$, $\tau = 1.8$, $a = 10$ and $b = 0.5$. The auto-covariance was calculated numerically as the inverse-Fourier transform of the spectral density.}
\end{figure}

Notice that 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 for any $\omega \neq 0$.

The following figure gives a sample path of the population process $\{X(t)\}$ obtained by numerical integration of the differential equation (20).

\begin{figure}
\centering
\includegraphics[width=\textwidth]{figure2.png}
\caption{Sample path of $\{X(t)\}$ for the same parameter values as in the previous figure. The dashed line indicates the value of $\bar{X}$.}
\end{figure}

The presence of a periodic component with frequency $\omega = \pm 3$ in the sample path may not be very obvious. Still, it is there. We can exploit the ergodicity of the population process to calculate the auto-covariance and spectral density also directly from the "data", i.e.,
from the sample path: Given the sample path \( \{x(t)\} \) for \( t \in (t_1, t_2) \), the average \( \bar{X} \) can be calculated as the time-average
\[
\bar{X} \approx \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} x(t) \, dt
\]
and the auto-covariance as the time-average
\[
C_X(\tau) \approx \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} (x(t + \tau) - \bar{X})(x(t) - \bar{X}) \, dt
\]
and using the Wiener-Khinchin theorem, the spectral density as the time-average
\[
S_X(\tau) \approx \left( \frac{1}{t_2 - t_1} \right) \left| \int_{t_1}^{t_2} (x(t) - \bar{X})e^{-i\omega t} \, dt \right|^2
\]
as illustrated in the following figure.

\begin{figure}[h]
\centering
\includegraphics[width=\textwidth]{figure3.png}
\caption{The auto-covariance and spectral density estimated from the sample path \( \{x(t)\} \).}
\end{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.