Populations dynamics

Math 392 - Mathematical Models in Biology

April, 2014
Exponential growth models

$B_n$ - the size of the population at the sampling time $n = 0, 1, 2, ...$

We expect to have

$$B_{n+1} = rB_n,$$

Here $b$ is the intrinsic growth rate. Taking the limit $h \to 0$, gives

$$\frac{dP}{dt} = bP(t).$$
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Take small sampling intervals $h$, and let $r = 1 + bh$.

Let $B_n = P(nh)$, where $P$ is a continuous function. Then $B_{n+1} = rB_n$ leads to

$$P(t + h) = rP(t) = (1 + bh)P(t)$$
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$$\frac{P(t + h) - P(t)}{h} = bP(t)$$

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Doubling time

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\]

For the doubling time \( t = T \), we have

\[ P(T) = 2P(0) = e^{bt}P(0) \]

\[ e^{bT} = 2 \Rightarrow T = \frac{\log 2}{b} \]

\[ P(nh) = B_n = r^nB_0 = r^nP(0) \Rightarrow r^n = e^{b\cdot nh} \]

\[ T = nh \log \frac{2}{\log r} \]

\( r \) can be estimated from observed data as

\[ r \approx \frac{B_1}{B_0} \]
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\[\Rightarrow T = \log_2 b\]

\[
rn = \frac{B_1}{B_0} = \frac{e^{bnh}b}{1} \log_2 r\]

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\( r \) can be estimated from observed data as \( r \approx B_1/B_0 \).
Least Squares estimation of \( r \)
Want to fit a line \( y = ax + b \) to the data points \( \{(x_i, y_i)\}_{i=1}^N \).
Least Squares estimation of $r$

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To do this minimize the square-error

$$L(a, b) = \sum_{i=1}^N [y_i - (ax_i + b)]^2.$$
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Using the notation $\langle q \rangle = \frac{1}{N} \sum_{i=1}^{N} q_i$, the solution will be

$$a = \frac{\langle xy \rangle - \langle x \rangle \langle y \rangle}{\langle x^2 \rangle - \langle x \rangle^2}, \quad b = \frac{\langle x^2 \rangle \langle y \rangle - \langle x \rangle \langle xy \rangle}{\langle x^2 \rangle - \langle x \rangle^2}$$
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$$\log B_n = (\log r)n + \log B_0.$$
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$$\log B_n = (\log r)n + \log B_0.$$  

Then $(\log r)$ can be found by the least-square fitting of the above line to the data

$$\{(n, \log B_n)\}_{n=0}^{N}.$$
Fibonacci bacteria

Bacteria with a lethal marker:
- a cell with 0 marks divides into a cell with 0 marks and another cell with 1 mark
- a cell with 1 mark divides into a cell with 0 marks and another cell with 2 marks
- a cell with 2 marks is unable to reproduce
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$B^0_n$ - the population of *clean* cells, $B^1_n$ - the population of cells with 1 mark.

<table>
<thead>
<tr>
<th>$n$</th>
<th>$B^0_n$</th>
<th>$B^1_n$</th>
<th>$B^2_n$</th>
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<tbody>
<tr>
<td>0</td>
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<td>0</td>
<td>0</td>
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<tr>
<td>1</td>
<td>1</td>
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<td>2</td>
</tr>
<tr>
<td>5</td>
<td>8</td>
<td>5</td>
<td>3</td>
</tr>
</tbody>
</table>

$B^0_n = B^0_{n-1} + B^1_{n-1}$

$B^1_{n-1} = B^0_{n-2}$

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1, 1, 3, 5, 8, 13, 21, ...
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$$r^2 - r - 1 = 0 \implies r_{1,2} = \frac{1 \pm \sqrt{5}}{2}.$$
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So a better fit will be

$$B_n = ar_1^n + br_2^n.$$ 

To find $a$, $b$, use $B_0 = 1$, $B_1 = 1$:

$$a = \frac{1 + \sqrt{5}}{2\sqrt{5}}, \quad b = \frac{\sqrt{5} - 1}{2\sqrt{5}}.$$
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- $B_n$ is always an integer
- $B_n / B_{n-1} \rightarrow r_1 = \frac{1 + \sqrt{5}}{2} \approx 1.618$ as $n \rightarrow \infty.$
Euler’s renewal theory

Divide the population into age classes that are census interval long. $B_n$ is the number of female births in the $n^{th}$ census interval.
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The renewal equation is

$$B_n = h_n + b_1 \lambda_1 B_{n-1} + b_2 \lambda_2 B_{n-2} + \cdots + b_n \lambda_n B_0.$$  

where $h_n$ is the births in the $n^{th}$ interval to those born before the first census.
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Fibonacci’s is a particular case, with

$$\lambda_1 b_1 = \lambda_2 b_2 = 1, \text{ and } \lambda_j b_j = 0 \text{ for all } j \geq 3; \quad h_n \equiv 0.$$
Renewal theorem
Assume fertility age of $M$ census intervals, i.e. $b_k = 0$ for $k > M$. 
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Then for $n > M$

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Fitting the exponential model $B_n \approx r^n$ to this equation results in the characteristic equation

$$r^n = b_1 \lambda_1 r^{n-1} + b_2 \lambda_2 r^{n-2} + \cdots + b_M \lambda_M.$$
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This has $M$ roots, $r_1, r_2, \ldots, r_M$, and a better model is

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Theorem
Let $p = \sum_{k=1}^{M} b_k \lambda_k$ be the maternity parameter, then

- If $p < 1$, then $B_n \to 0$ as $n \to \infty$, i.e. the population dies out if each mother less than replaces herself.

- If $p \geq 1$, then there is a unique root $r = r^*$ of the characteristic equation, such that all other roots satisfy $|r| < r^*$ and $B_n \approx C(r^*)^n$ as $n \to \infty$. 

$\dot{P} = bP$. 

What if $b = b(S)$ depends on the substrate $S$?

$$b(S) = \frac{V S}{K + S}$$

$V$ - max uptake rate ($\lim_{S \to \infty} b = V$)

$K$ - saturation constant ($\text{when } S = K, \text{uptake rate } = \frac{V}{2}$)

$Y$ - yield (measure by how much the population grows for each unit of $S$)

$$d\left(\frac{YS + P}{P(0) + YS(0)}\right) = 0 \implies P = -YS + (P(0) + YS(0)).$$
Microbial biology

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\begin{cases}
\dot{P} & = \frac{VS}{K+S} P \\
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\[ \dot{P} \approx \frac{VS(0)}{K + S(0)} P, \quad \dot{S} \approx -\frac{V[P(0) + YS(0)]}{KY} S \]
Let $C = P(0) + YS(0)$, then

$$S = \frac{C - P}{Y}, \quad \text{and} \quad \dot{P} = \frac{V(C - P)}{KY + C - P}P$$
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$$S = \frac{C - P}{Y}, \quad \text{and} \quad \dot{P} = \frac{V(C - P)}{KY + C - P}P$$

Using linear approximation for the rate $b = \frac{V(C - P)}{KY + C - P}$, we have the logistic equation

$$\dot{P} = b^* \left( 1 - \frac{P}{K^*} \right) P,$$

where

$$b^* = \frac{VC}{KY + C}, \quad K^* = \frac{C}{YK}.$$
Quiescence

\[
\begin{align*}
\dot{S} &= -\frac{V S}{K + S} \frac{P}{Y} \\
\dot{P} &= \frac{V S}{K + S} P - \alpha(S) P + \beta(S) Q \\
\dot{Q} &= \alpha(S) - \beta(S) Q
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- \( S \) high \( \Rightarrow \alpha(S) \approx 0, \beta(S) > 0; Q \leftrightarrow P \)
- \( S \) low \( \Rightarrow \alpha(S) > 0, \beta(S) \approx 0; P \leftrightarrow Q \)
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Cells grow in a chamber with medium that is constantly renewed by the flow of media through it.

the washout rate, \( w = \frac{\text{Flow (volume/time)}}{\text{Volume}} \)
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Balance of masses then gives

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\begin{align*}
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In this case

\[
\frac{d}{dt}(YS + P) = w(YS(0) - YS - P),
\]

so

\( YS + P \to YS(0) \quad \text{as} \ t \to \infty. \)
YS + P → YS(0) as $t \to \infty$

can happen by either

- cells washing out of the chamber, so $S \to S_0$, or
- dynamic equilibrium is reached
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A dynamic equilibrium will be reached when

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which is possible only if \( V > w \), i.e. the uptake velocity is greater than the washout rate.
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Nonlinear reproduction curves
Consider a more general discreet model, with intrinsic growth rate \( r = r(B) \)

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Verhulst’s Model (Beverton-Holt)

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B_{n+1} = \frac{2}{1 + B_n/K}B_n, \quad \text{where} \quad r(B) = \frac{2}{1 + B/K}
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so \( r \approx 2 \) for small \( B \), and the population less than reproduces itself for large \( B \).
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Analytic iteration: denote \( R_n = \frac{1}{B_n} \), then

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R_{n+1} = \frac{R_n}{2} + \frac{1}{2K} = \frac{R_{n-1}}{2} + \frac{1}{2K} + \frac{1}{2K}
\]

\[
= \frac{1}{2^{n+1}} R_0 + \frac{1}{2K} \left( 1 + \frac{1}{2} + \cdots + \frac{1}{2^n} \right) = \frac{1}{2^{n+1}} R_0 + \frac{1}{K} \left( 1 - \frac{1}{2^{n+1}} \right).
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\]

We see that
- \( R_n \rightarrow \frac{1}{K} \) as \( n \rightarrow \infty \),
- \( R_n \left( \frac{1}{2^n} \right) \) is linear, can use least-squares to estimate \( K \).
Cobwebbing analysis

The dynamics can be studied geometrically from the graph of the reproduction function

\[ F(B) = r(B)B = \frac{2B}{1 + B/K} \]
Cobwebbing analysis

The dynamics can be studied geometrically from the graph of the reproduction function

$$F(B) = r(B)B = \frac{2B}{1 + B/K}$$

Cobwebbing of Verhulst’s model

Verhulst’s with predation
Cobwebbing analysis

The dynamics can be studied geometrically from the graph of the reproduction function

\[ F(B) = r(B)B = \frac{2B}{1 + B/K} \]

Cobwebbing of Verhulst’s model

Verhulst’s model can be modified to add predation, for example, leading to

\[ F(B) = \frac{rB^2}{1 + (B/K)^2}, \]

for which the equation \( F(B) = B \) has 3 roots.