Discrete population models

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Rational: cyclic (seasonal) timing of reproduction and development, synchronization

Topics:

1. Renewal models (Fibonacci)
2. Discrete logistic models (Verhulst vs. Ricker); cobwebs; equilibria, cycles, chaos
3. Discrete-delay models:
    a. Delayed Ricker
    b. IWC whale model
    c. Tumor growth

Renewal/growth models; Fibonacci

Fibonacci sequence:

$$x_{n+1} = x_n + x_{n-1};\ x_0 = 0; x_1 = 1 \tag{0.1}$$

defines second order linear *recurrence*, or *finite difference* equation. Like higher order DEs such difference equations can be converted to a matrix system

$$X_{t+1} = AX_t;\ \text{with } X_t = \begin{pmatrix} x_{t-1} \\ x_t \end{pmatrix}; \text{matrix } A = \begin{bmatrix} 0 & 1 \\ 1 & 1 \end{bmatrix} \tag{0.2}$$

It can be viewed as two-stage population system: x_t - young, y_t - adults, that grows (renews) as

$$x_{t+1} = y_t;\ y_{t+1} = y_t + x_t$$

in unit time step. More natural discrete time step 2-stage model obeys

$$x_{t+1} = by_t;\ y_{t+1} = s_y x_t + s_a y_t;\ \text{with matrix } A = \begin{bmatrix} 0 & b \\ s_y & s_a \end{bmatrix} \tag{0.3}$$

where $b > 0$ - proliferation (growth) factor, $0 < s_{y,a} < 1$ - survival fractions (of young and adults), so $\mu_{y,a} = 1 - s_{y,a}$ - mortality factors. Stability of solutions (0.2) $X_n = A^n X_0$, depends on eigenvalues of matrix A

$$\lambda_{1,2} = \frac{s_a}{2} \pm \sqrt{\frac{s_a{}^2}{4} + b} = 1?$$

Show (i) unstable $\lambda_1 > 1$, corresponds to $s_y b > \mu_a$ (surviving young exceed adult death removal); (ii) stable (decay) gives $s_y b < \mu_a$.

A general finite difference equation

$$x_{t+m} = a_1 x_{t+m-1} + \ldots + a_m x_t \tag{0.4}$$

can also be solved by *characteristic polynomial*

$$p(\lambda) = \lambda^m - a_1 \lambda^{m-1} - \ldots - a_m$$

whose (complex) roots give special power solutions $\{\lambda_j^{\,n}\}$, and general one $x_n = \sum_{j=1}^{m} c_j \lambda_j^{\,k}$,

in particular, Fibonacci numbers: $x_n = \dfrac{\lambda_1^{\,n} - \lambda_2^{\,n}}{\lambda_1 - \lambda_2}; \lambda_{1,2} = \dfrac{1 \pm \sqrt{5}}{2}$.

Verhulst and Ricker Discrete Logistic Models.

They offer two different ways to discretize continuous logistic model:

$$y' = r(1 - y/N)\, y \tag{0.5}$$

in time steps Δt, so $t_n = n\Delta t,$ and $y_n = y(t_n)$.

Verhults discretizes derivative: $y_{n+1} - y_n \approx r(1 - y_n/N)\, y_n \Delta t$, whence

$$y_{n+1} = r^* \left(1 - y_n / N^*\right) y_n; \text{ with } r^* = 1 + r\Delta t, N^* = \frac{1 + r\Delta t}{r\Delta t} N \tag{0.6}$$

Ricker solves (0.5) over short time $[t_n, t_n + \Delta t]$, assuming “near constant” rate coefficient

$r(1 - y/N) \approx r(1 - y_n/N)$, to get

$$y_{n+1} = r^* y_n e^{-y_n/N}; \; r^* = e^{r\Delta t} \tag{0.7}$$

In both cases rescaled variable $u = y/N$ solves a nonlinear 1-st order recurrence:

$$u_{n+1} = f(u_n); \text{ where } f(u) = \begin{cases} ru(1-u) & \text{- quadratic (Verhulst)} \\ rue^{-u} & \text{- Ricker} \end{cases} \tag{0.8}$$

Verhulst population model does not allow values above threshold N (unrealistic), while Ricker has no such limitations (more realistic).

Solution of (0.8) are made of iterates of map f: $u_n = \underbrace{f(f(\ldots f(u_0)))}_{n \text{ times}}$. Special cases include

(i) equilibria: $u = f(u)$ - fixed points of f;

(ii) m- cycles (periodic orbits): $u_{t+m} = u_t$ - fixed points of $f_m(u) = \underbrace{f(f \ldots f(u))}_{m}$;

(iii) chaotic trajectories.

Stability of equilibrium u_0, or cycle $\{u_0, u_1, \ldots u_{m-1}\}$ is determined by linearized model:

$$u_{t+1} = Bu_t; \text{ where } B = f'(u_0), \text{ or } f_m'(u_0) \text{ (for cycle)} \tag{0.9}$$

So $B < 1$ are stable, and $B > 1$ (unstable).

Discrete logistic models (0.8) exhibit a complex chain of bifurcations in terms of growth parameter $r > 1$, that progresses from stable equilibria to limit cycles of different periodicities to chaos. They are summarized in the following table:

$1 < r < 3$	stable equilibrium $y^* = 1 - 1/r$
$3 < r < r_4$	stable period : 2 orbit
$r_4 < r < r_8$	period doubling : 2^2 – orbit
...	□
$r_k < r < r_{k+1}$	stable 2^k – orbit
...	□
$r_3 < r < r_{3,1}$	stable 3 – orbit
...	□
$r_{3,k} < r < r_{3,k+1}$	3 2^k – orbit
...	□
$r_c < r$	chaos

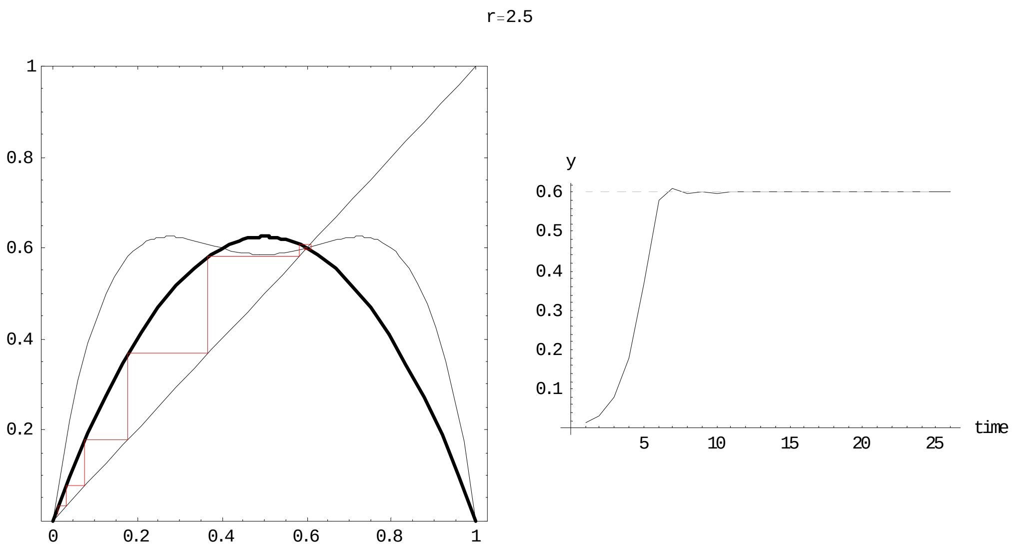
Two important types of bifurcations that occur in iterated maps are *period doubling* illustrated in Fig. 1, and *tangential* bifurcation (e.g. period 3 cycle, or any other odd m). In *period doubling* a stable m-cycle (i.e. fixed point y^* of $f_m(y)$) looses stability for $f_{2m}(y)$, but a new stable pair $\{y_1^* < y^* < y_2^*\}$ (2-cycle of f_m) comes in place. So *period doubling* serves as a discrete version of *pitchfork bifurcation*: "stable equilibrium" $\rightarrow$"stable-unstable-stable triplet".

Tangential bifurcation (triple cycle) is illustrated in Fig.2: three stable fixed points of f_3 come out of the complex domain at critical $r_3 = 3.828$, and develop into stable period-3 cycle of $f(y)$ in the range $r_3 < r < r_6$, when another period doubling occurs. Fig.3 shows critical case r_3 and period-3 cycle.

Problem: Show that m-cycle $\{y_1, \ldots, y_m\}$ of map $f(y)$ is stable if and only if the corresponding fixed point of the m-th iterate $f_m(y)$ is stable. Hint: linearize f about m- cycle, and show that the resulting linear system is given by a Leslie type (cyclic) matrix with entries $a_j = f'(y_j)$

$$A = \begin{bmatrix} 0 & \ldots & & a_m \\ a_1 & 0 & \ldots & 0 \\ 0 & a_2 & & 0 \\ 0 & \ldots & a_{m-1} & 0 \end{bmatrix}$$

Use characteristic polynomial $\det(\lambda - A) = \lambda^m \pm a_1 \ldots a_m$, and link stability of A to stability of fixed points of f_m.



(a)

(b)

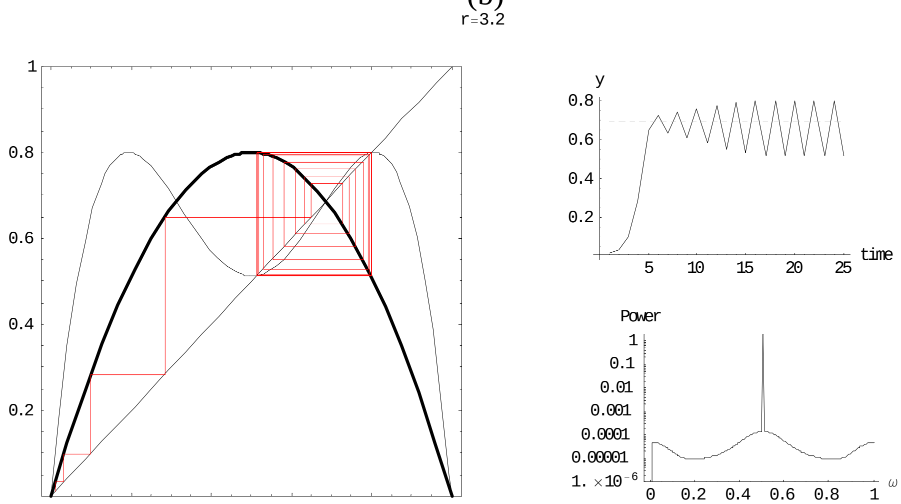


Fig.1: Period doubling: Plot (a) stable equilibrium $y^* = 1 - 1/r;\ (1 < r < 3)$ for $f(x)$ and $f_2(x) = f(f(x))$, turns Plot (b) into stable 2-cycle $\{y_1^* < y^* < y_2^*\}$, so that $f'(y^*) > 1;\ f'(y_i^*) < 1$.

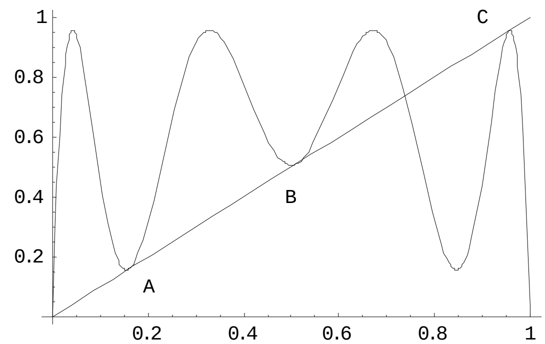
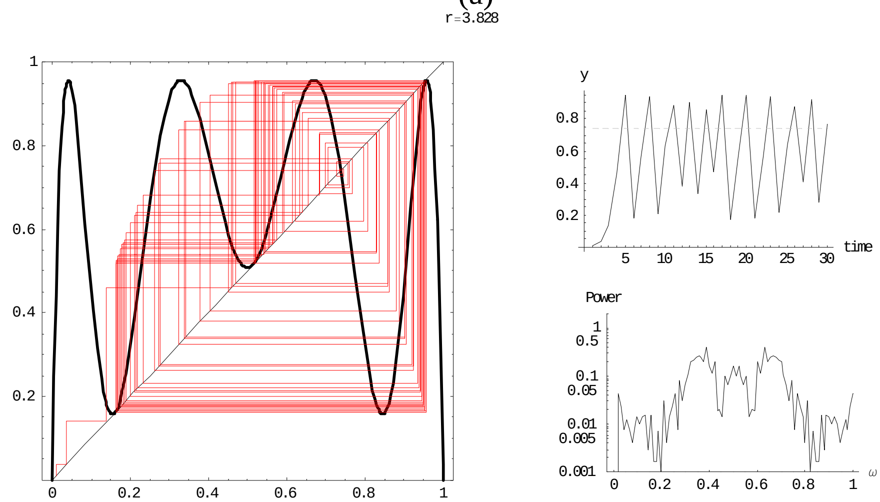


Fig. 2: Tangential bifurcation at $r_3 = 3.828$

(a)



(b)

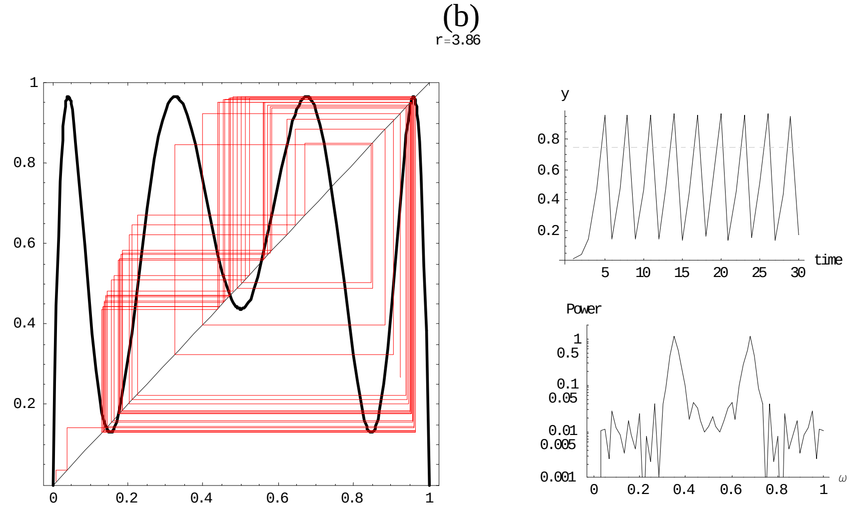


Fig.3: Dynamics of quadratic map in two cases: (a) critical $r_3 = 3.828$; (b) stable 3-cycle.

Further details and computations are given in Mathematica notebook.

Fourier Power Spectra

Periodic or chaotic (time series) solution can be examined by Fourier methods (power spectra) discussed in the notebook. We recall that a (generalized) *Fourier expansion*

$f(t) \sim \sum_{k=-\infty}^{\infty} \hat{f}_k e^{2\pi i \omega_k t}$, consists of (amplitude) coefficients $\{\hat{f}_k\}$, and frequencies $\{\omega_k\}$. For periodic functions f with period T, all frequencies are multiples (harmonics) of the lowest one: $\omega_k = k\omega_1;\ \omega_1 = \frac{2\pi}{T}$, and coefficients

$$\hat{f}_k = \int_0^1 f(t) e^{-2\pi i k t} dt = \langle f \mid e^{2\pi i k t} \rangle$$

- (square-mean) inner product of f and exponent.

More general *quasi-periodic* functions have arbitrary set of ω's. Frequencies $\{\omega_k\}$ define *power spectrum* $\left\{ \left| \hat{f}(\omega) \right|^2 \right\}$ of signal $f(t)$. So spectral peaks in Fig. 1,3 (right bottom) indicate the most important frequencies that appear in long term series if iterates $\{y_k\}$. One can see frequencies $\omega = 1/2; 1/3; \ldots$ corresponding to 2-cycles, 3-cycles, etc.