

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:

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

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

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

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

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

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

$$x_{t+m} = a_1 x_{t+m-1} + \dots + a_m x_t \quad (0.4)$$

can also be solved by *characteristic polynomial*

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

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

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

Verhulst and Ricker Discrete Logistic Models.

They offer two different ways to discretize continuous logistic model:

$$y' = r(1 - y/N)y \quad (0.5)$$

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

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

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

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

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

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

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

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 $f : u_n = \underbrace{f(f(\dots f(u_0)))}_{n \text{ times}}$. 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 $f_m(u) = \underbrace{f \dots f}_m(u)$;

(iii) chaotic trajectories.

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

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

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 $f_m(y)$) loses 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 $\{y_1, \dots, y_m\}$ 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 $a_j = f'(y_j)$

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

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

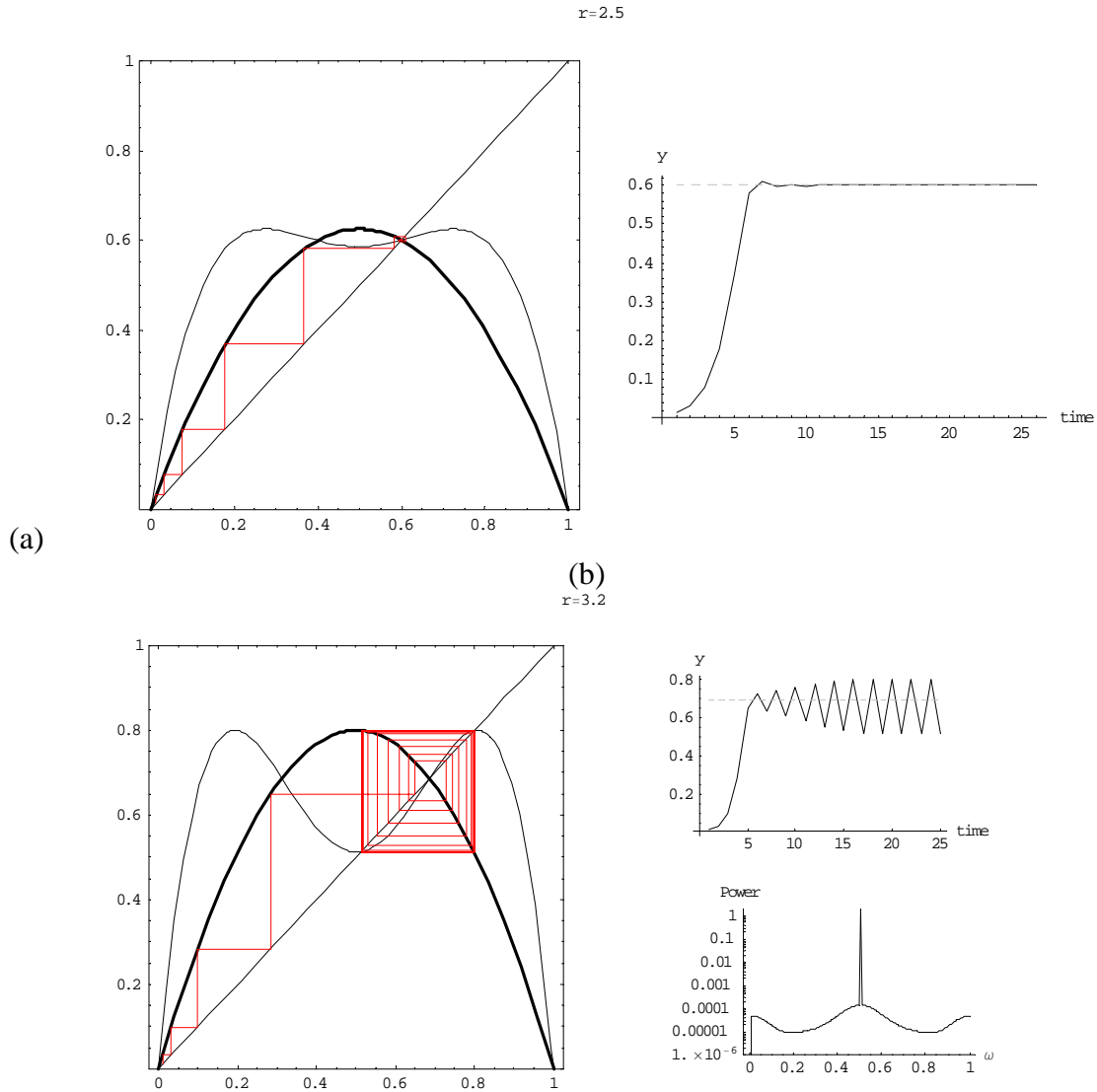


Fig.1: Period doubling: Plot (a) stable equilibrium $y^* = 1 - 1/r$; ($1 < r < 3$) for $f(x)$ and $f_2(x) = f(f(x))$, turns Plot (b) into stable 2-cycle $\{y_1^* < y^* < y_2^*\}$, so that

$$f'(y^*) > 1; f'(y_i^*) < 1.$$

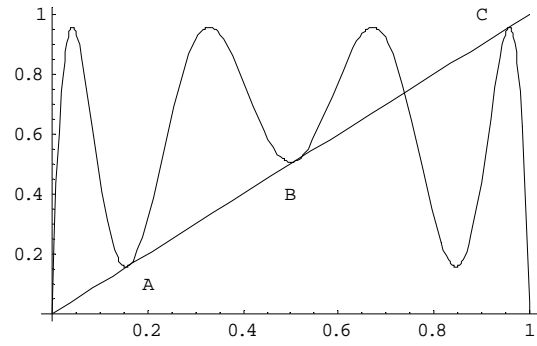
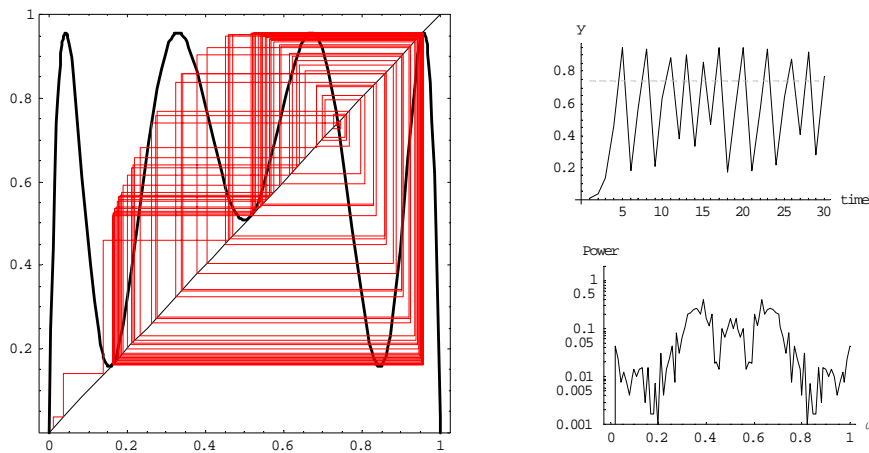


Fig. 2: Tangential bifurcation at $r_3 = 3.828$

(a)

$r=3.828$



(b)

$r=3.86$

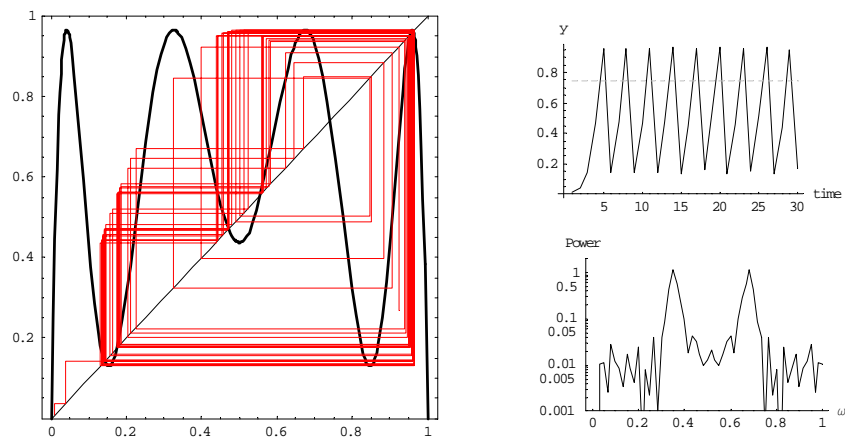


Fig.3: Dynamics of quadratic map in two cases: (a) critical $r_3 = 3.828$; (b) stable 3-cycle.

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

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

- (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 $\omega = 1/2; 1/3; \dots$ corresponding to 2-cycles, 3-cycles, etc.