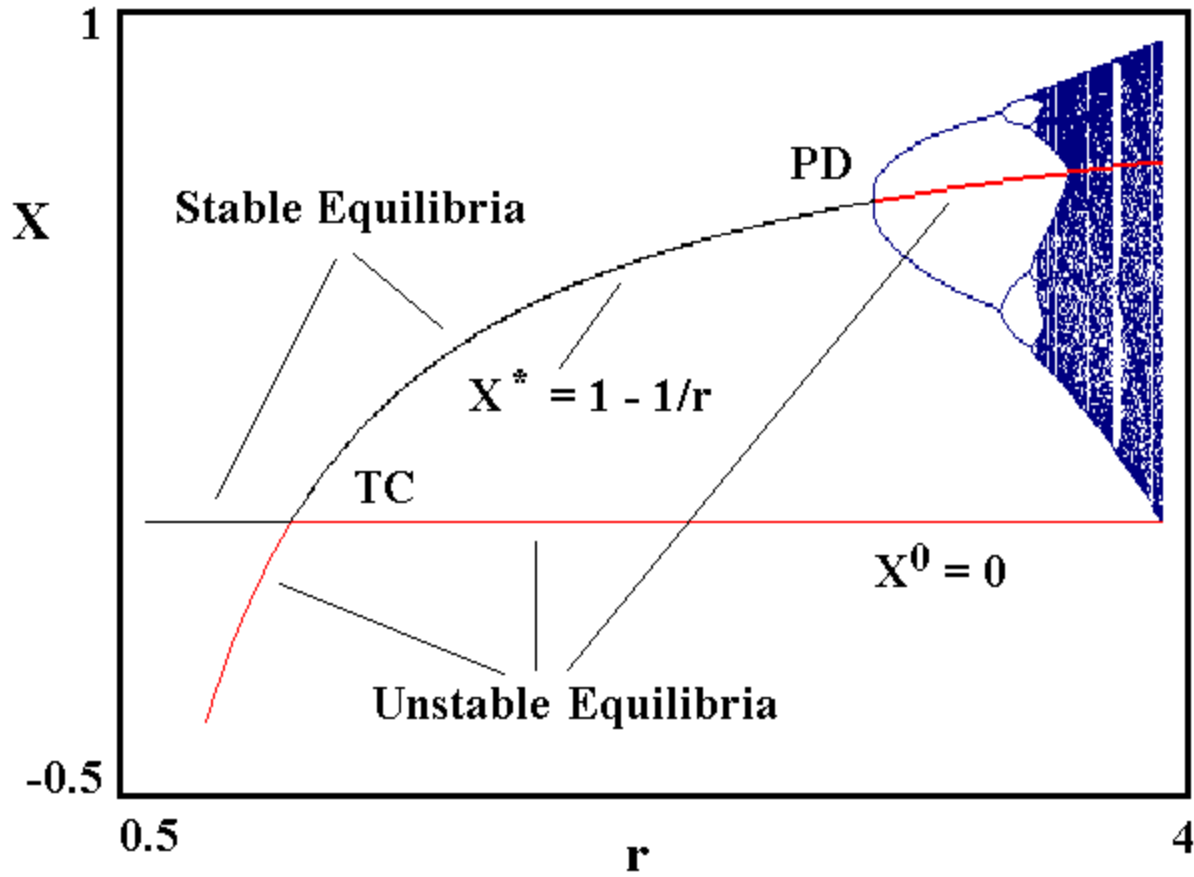


Ecology 302. Lecture IV.

(Gotelli, Chapter 2; Ricklefs, Chapter 11; Hannesson)



Bifurcation diagram for the logistic map. The long-term dynamics are plotted for 452 parameter values on the interval, $r = [0,1]$. At $r = 0$, the two equilibria, X^0 and X^* collide and exchange stability. At $r = 4$, the “attractor” (blue points) collides with X^0 and loses stability. For $r > 4$, “almost all” initial conditions diverge to $-\infty$.

Key Points.

- In a finite environment, exponential growth eventually checked by increased mortality / reduced reproduction – “density dependence”.
- Logistic Equation.
 - Simplest model assumes the *per capita* rate of increase declines linearly.
 - Two equilibria: $N = 0$ and $N = K$ (carrying capacity).
- Logistic growth commonly observed in the laboratory; less frequently in nature.
 - Gause’s yeast experiments a classic example of ~ logistic growth in the lab – population limited by increasing concentration of alcohol (product of glycolysis).
 - Soay sheep manifest approximately logistic growth with fluctuations about carrying capacity.
 - Fluctuating densities of song sparrows interpreted as density dependence in the face of environmental fluctuations.

- Stability.
 - An equilibrium of a single variable **continuous** system is stable if the eigenvalue, λ , associated with **that** equilibrium is **negative**.
 - An equilibrium of a single variable **discrete** system is stable if the eigenvalue, μ , associated with **that** equilibrium is **less than 1 in magnitude**, *i.e.*, $-1 < \mu < 1$.
 - This is because deviations, $x(t)$, from equilibrium grow according to

$$x(t) = x_0 e^{\lambda t} \text{ (continuous system)}$$

$$x_t = x_0 \mu^t \text{ (discrete system)}$$

- Harvesting.
 - There is a maximum harvesting rate, H_{max} , beyond which population collapses to zero.
 - For lower harvesting rates, there are three equilibria.
 - $N = 0$ and N^* (stable).
 - $0 < N^\ddagger < N^*$ (unstable)

- Harvesting at H_{max} generates the **maximum sustained yield** (MSY).
- Harvesting at or near H_{max} is **risky** because slight environmental deterioration \Rightarrow population collapse.
- *El Niño*-caused collapse of Peruvian anchovy an example.
- If harvesting rate varies slowly in response to changes in yield, a two-variable system (H, N) can be approximated by a single variable system (H) .
- Time delays are destabilizing.
- The discrete logistic equation manifests a variety of behaviors (equilibria, cyclic, chaotic) depending on the value of r .
- Chaotic systems are inherently unpredictable.
 - Nearby trajectories separate exponentially.
 - Given *any* level of observational error, long-term forecasting **impossible**.
 - All that can be specified is a probability distribution.

- Hassel, Lawton, May estimated stability behavior of ~30 lab and field populations.
 - Estimated parameter values of a single species difference equation similar to, but more realistic than, the discrete logistic.
 - Concluded non-equilibrium dynamics rare.
- But –
 - Many examples of natural populations manifest sustained, more or less regular, fluctuations.
 - Parameter estimates based on reproduction / survival of single species at a fixed point in time (or over a fixed (usually brief) interval), **ignores** the web of interactions in which **all** species are embedded.

I. Logistic Equation.

A. If permitted to grow unchecked by accumulating waste products, predation or disease, populations eventually limited by lack of resources.

1. Birth rate ↓ and / or death rate ↑.

B. Simplest assumption is that *per capita* rate of reproduction declines linearly. Thus

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) \quad (1)$$

where K is the “carrying capacity of the environment.”

C. Solution.

1. Eq 1 =>

$$\int_{N_0}^{N(t)} \frac{dN}{N(K - N)} = \frac{r}{K} \int_0^t d\tau . \quad (2)$$

which can be integrated to yield

$$N(t) = \frac{K}{1 + \left(\frac{K - N_0}{N_0} \right) e^{-rt}} . \quad (3)$$

2. Provided $N_0 > 0$,

$$\lim_{t \rightarrow \infty} N(t) = K \quad (4)$$

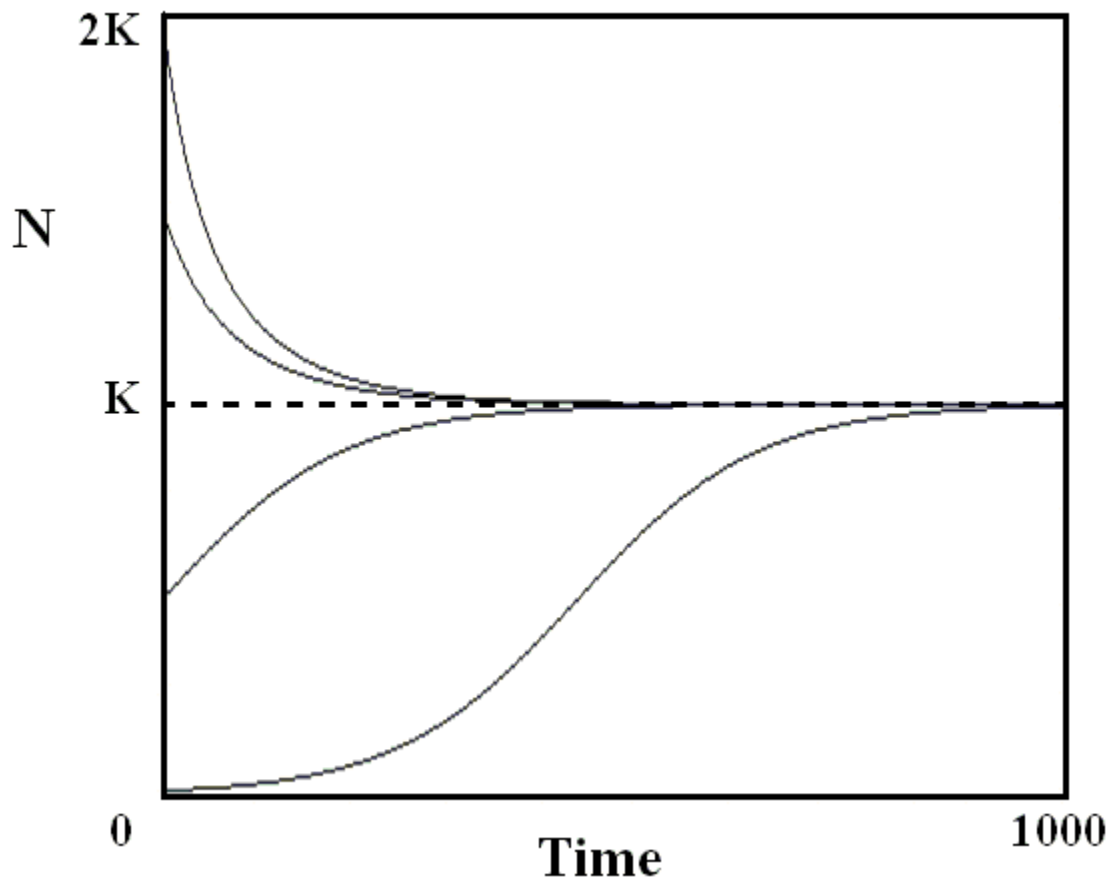


Figure 1. Logistic population growth (Eq 7) for $N_0 = .01K, 0.5 K, 1.5K$, and $1.9 K$. $r = .01$. Time units are arbitrary.

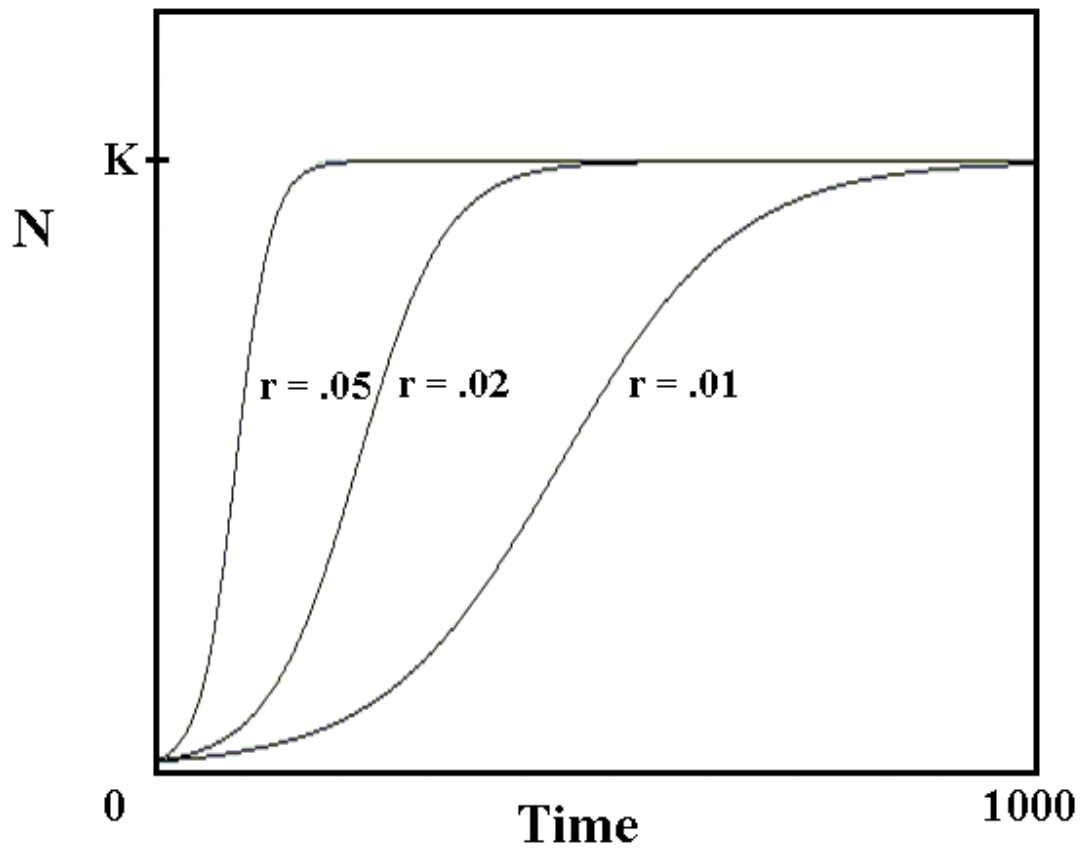


Figure 2. Logistic population growth (Eq 7) for different values of r . $N_0 = .01 K$. The rate of approach to equilibrium co-varies with r . Time units are arbitrary.

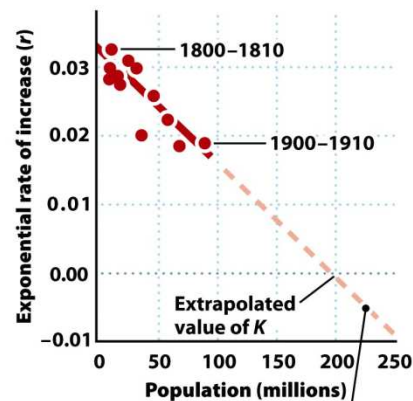
3. Historical Note.

1. The word “logistic” derives from the Medieval Latin, *logisticus*, which refers to “calculation.”

2. 1st used to model human populations by Pierre François Verhulst in 1838.

3. Rediscovered by Pearl and Reed who applied it to the US population in 1910.

4. Prediction failed miserably (Figure 3) – what can happen when you fit slowly accumulating data to the wrong model.



Dashed line is the extrapolation of the straight line (as described by the logistic equation)

Figure 11.13
The Economy of Nature, Sixth Edition
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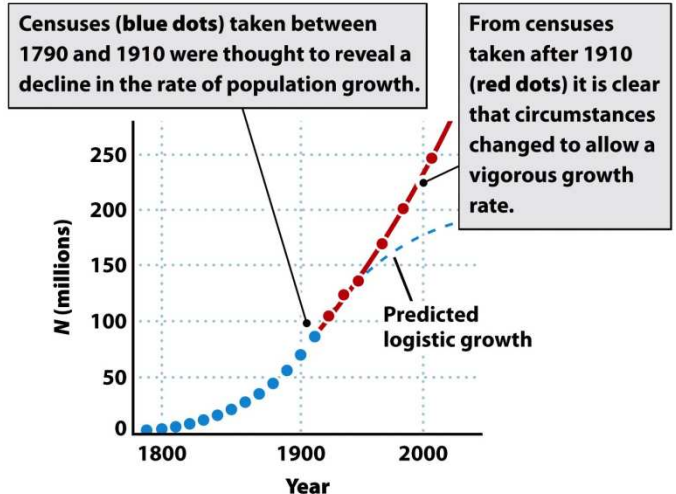


Figure 11.16
The Economy of Nature, Sixth Edition
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Figure 3. Top. Equation 4.2 fitted to U. S. population data from 1790 to 1910 suggested that the population would level off at about 200 million. Bottom. In the event, numbers continued to increase.

D. Logistic growth in the laboratory.

1. G. F. Gause studied population growth, competition and predation in laboratory microcosms.

a. Yeast cells metabolize sugar to ethyl alcohol (EtOH).

b. EtOH accumulates in medium – inhibits reproduction by killing newly-formed buds.

c. Continuing accumulation of EtOH indicates that at least some cells survive – *i.e.*, cessation of population growth not due to sugar exhaustion.

d. Density at which population growth ceases can be reduced by adding EtOH to the medium (Figure 5).

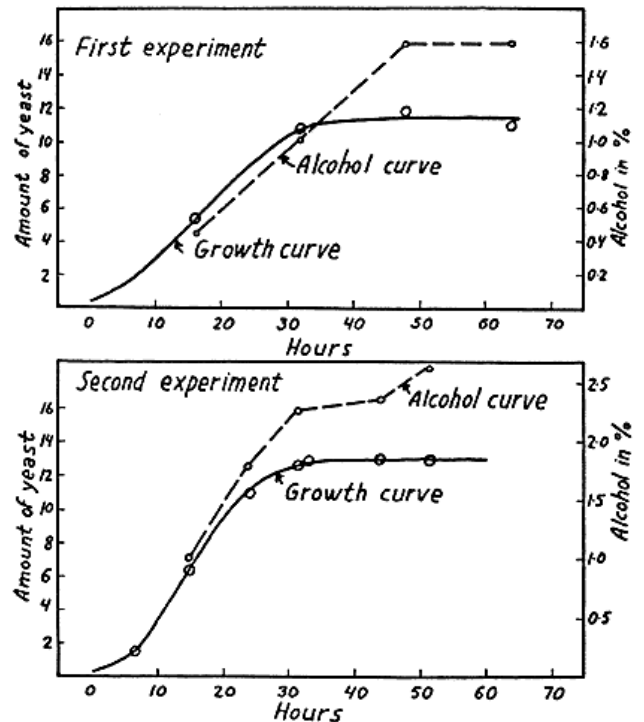


Figure 4. Experiments with yeast in laboratory microcosms. Alcohol continues to accumulate after reproduction ceases. From G. F. Gause. *The Struggle for Existence*.

2. In bacterial cultures one sees much the same thing.

a. Initial “lag” phase during which period the cells “gear up” – synthesize enzymes, *etc.*

b. Period of approximately exponential growth.

c. Sometimes called “log phase” *i.e.*, $N(t) = N_0 e^{rt} \Rightarrow \ln N(t) = \ln N_0 + rt$.

d. Thereafter, cell numbers plateau.

e. Finally, cell numbers decline as cells begin to die.

3. As in Gause’s yeast experiments, environmental deterioration **impedes reproduction first**, then kills adult organisms – a very general pattern – *i.e.*, greater sensitivity of reproduction and juveniles.

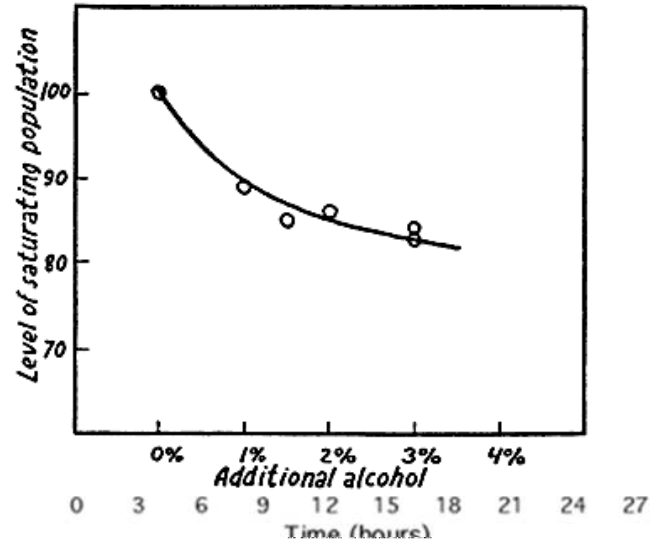
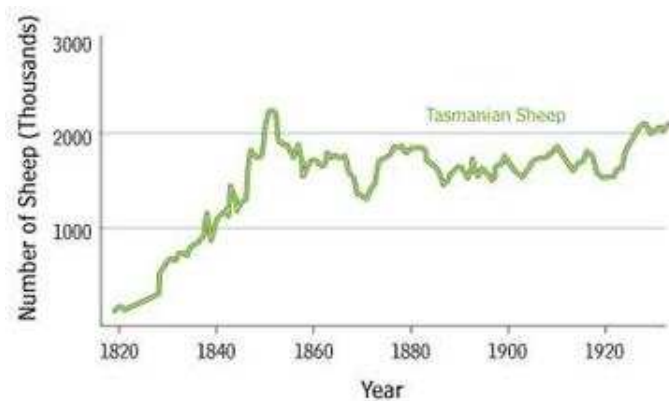


Figure 5. Effect of adding alcohol to yeast cells growing in a closed system. Each point represents a different experiment.

E. Logistic growth in nature.

1. Lots of lab examples; in real world, not so many.
2. “Examples” often manifest
 - a. Initial overshoot of “K”
 - b. Damped oscillations to “equilibrium”.
3. Overshoot and oscillations \Rightarrow other variables.
4. Continuing fluctuations often ascribed to exogenous perturbations and underlying density dependence.
5. Tasmanian sheep a frequently cited example (Figure 6).
6. An alternative is “boom and bust” (Figure 7).



Sheep population size on the island of Tasmania. Rainfall limits the amount of food available to the sheep. (Data from Davidson 1938.)

Figure 6. Tasmanian sheep population following introduction.

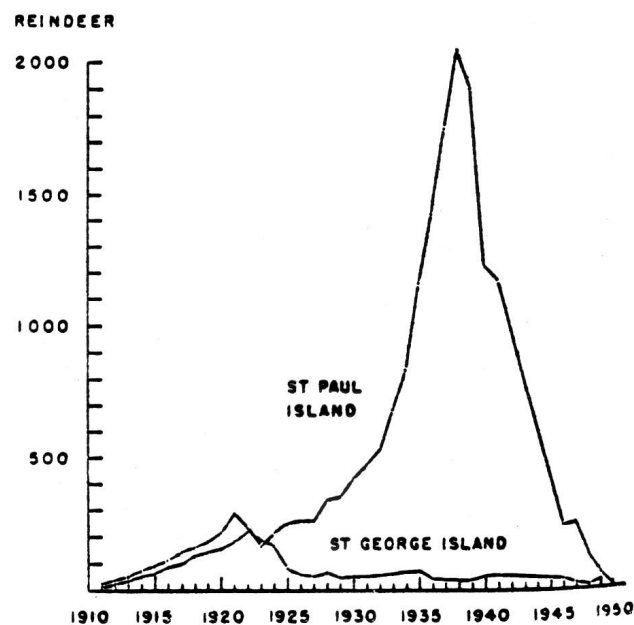


Figure 7. Pribilof Is. Reindeer. Data are combined number of deer killed and spared or, when no animals killed, the number counted.

F. Song sparrows of Mandarte Island (off British Columbia).

1. Fluctuating densities (Figure 8) reveal underlying density dependence (Figure 9).
 - a. Increasing numbers of males without territories.
 - b. Decreasing numbers of young fledged per female.
 - c. Decreasing juvenile overwinter survival.
2. Observation of density-dependence does not confirm logistic-like dynamics.

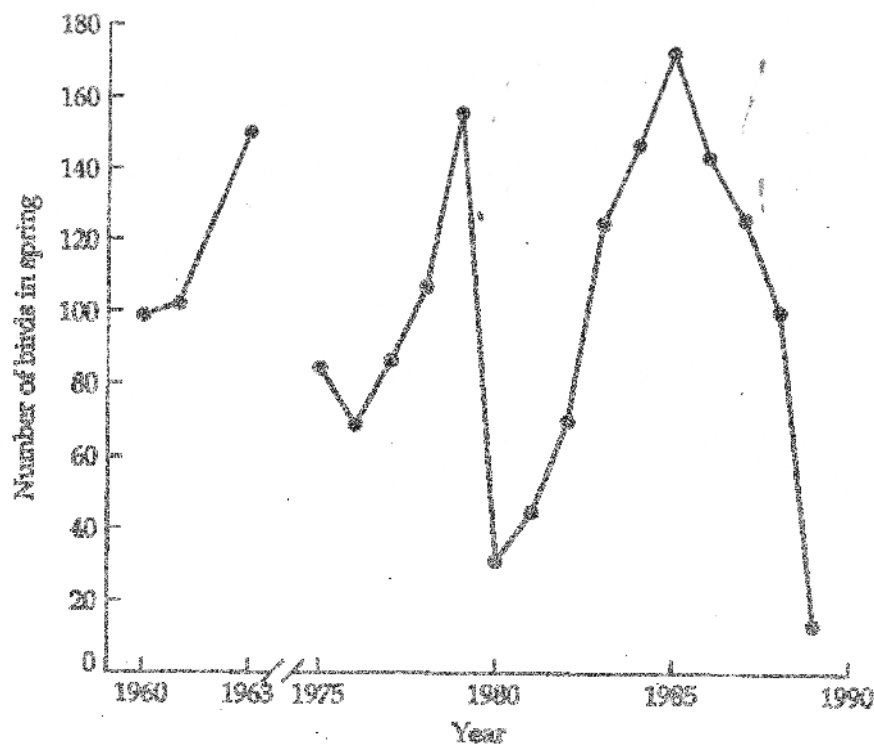


Figure 8. Fluctuating song-sparrow numbers on Mandarte Is.

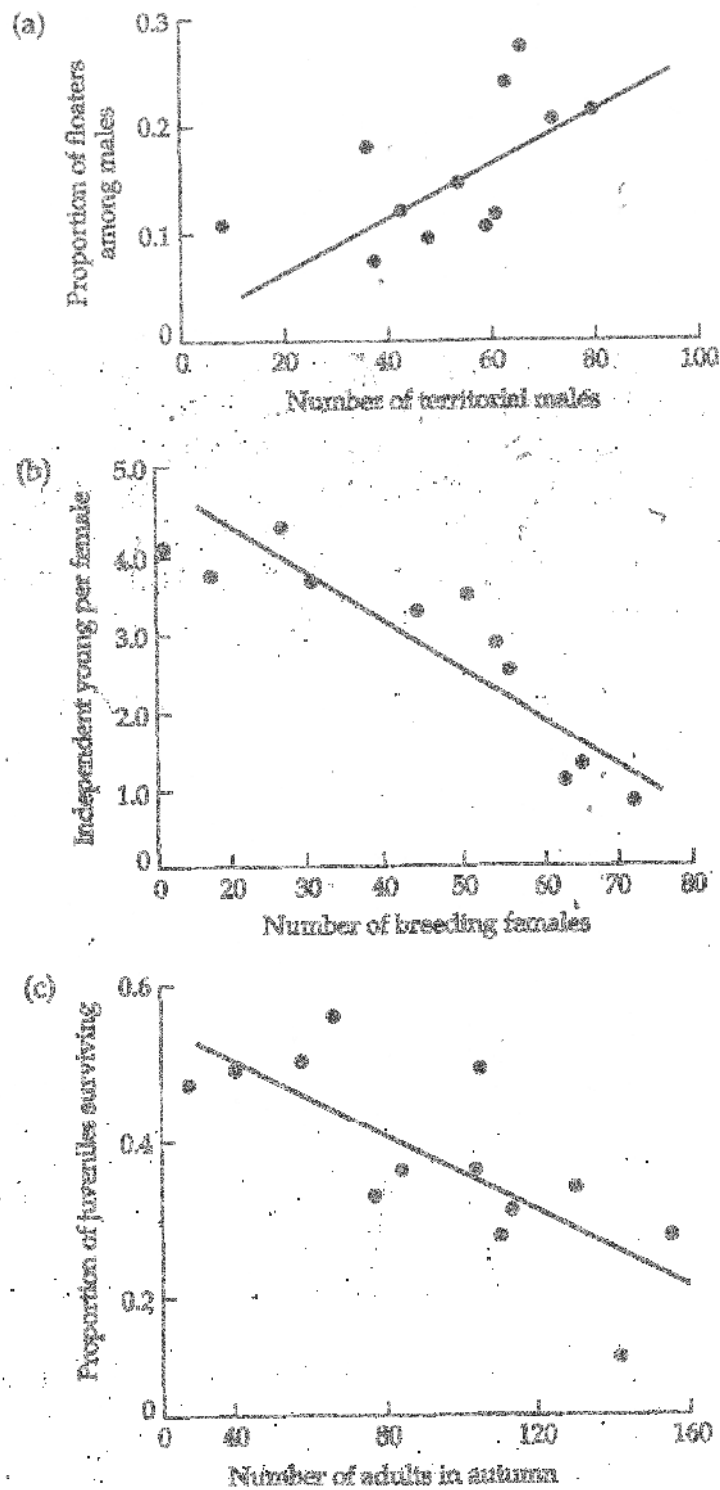


Figure 9. Density-dependent responses to changing numbers of song sparrows on Mandarte Island.

G.Stability

1. Plotting right side of Eq 5 vs. N yields a parabolic curve (Figure 10).
2. Two equilibria: $N = 0$ (unstable); $N = K$ (stable).
3. One can prove (obvious from the figure), that $N^* = K$ is stable with respect to all N_0 save $N_0 = 0$.

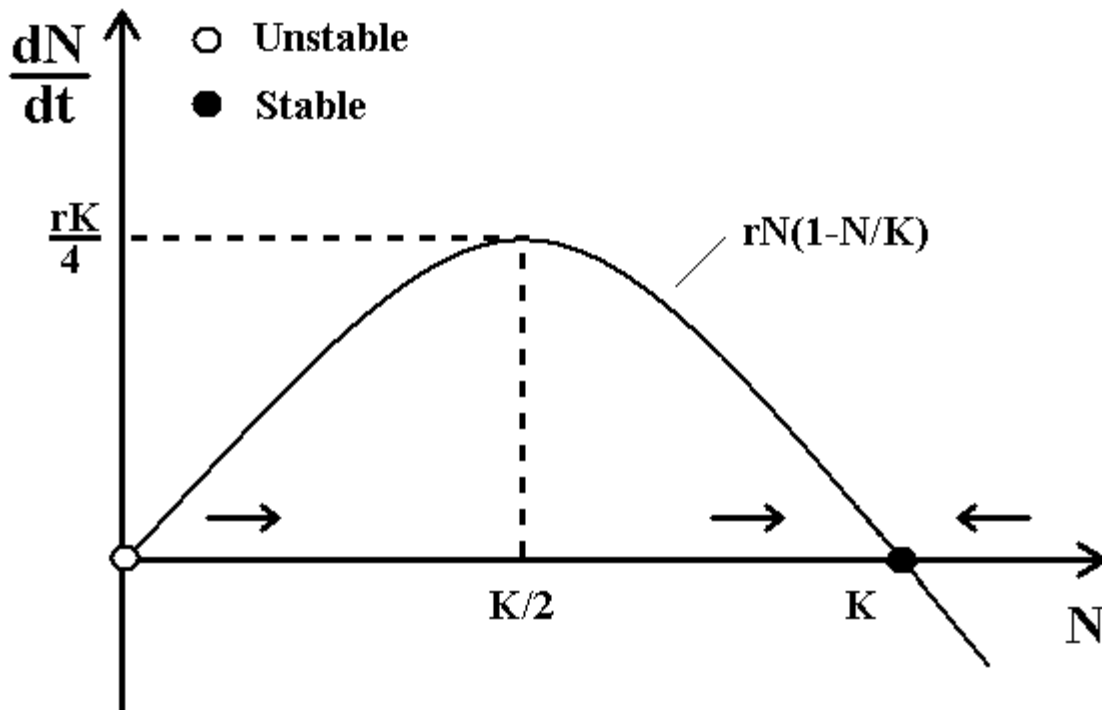


Figure 10. Logistic equation: Equilibria and stability.

H.Easy test for local stability in single variable systems.

1. An equilibrium, x^* , of a continuous equation

$$dx/dt = f(x) \quad (5)$$

is stable if the *eigenvalue*

$$\lambda = \left. \frac{df}{dx} \right|_{x=x^*} < 0 \quad (6)$$

2. An equilibrium, X^* , of a discrete equation

$$X_{t+1} = F(X_t) \quad (7)$$

is stable if $-1 < \mu < 1$, where the eigenvalue μ is given by

$$\mu = \left. \frac{dF}{dX} \right|_{X=X^*} \quad (8)$$

3. For the logistic

$$\lambda = \frac{d}{dN} \left[rN \left(1 - \frac{N}{K} \right) \right] \Big|_{N=N^*} = r \left(1 - \frac{2N}{K} \right) \Big|_{N=N^*} \quad (9)$$

where $N^* = 0$ or K .

4. Thus

$$\lambda = r, \quad N^* = 0 \quad (10)$$

$$\lambda = -r, \quad N^* = K$$

5. Note that **each equilibrium has its own eigenvalue.**

I. Eigenvalues and local stability.

1. Consider

$$\frac{dX}{dt} = f(X) \quad (11)$$

2. Let

$$x(t) = X(t) - X^* \quad (12)$$

be the deviation from equilibrium, X^* . Clearly,

$$\frac{dx}{dt} = \frac{dX}{dt} = f(X)$$

3. Approximate $f(X)$, with a straight line tangent to f at $X = X^*$. Note that $f(X^*) = 0$. Then

$$\frac{dx}{dt} \approx 0 + x \left. \frac{df}{dX} \right|_{X=X^*} = \lambda x \quad (13)$$

where λ is called an eigenvalue.

Linearizing a Nonlinear Map

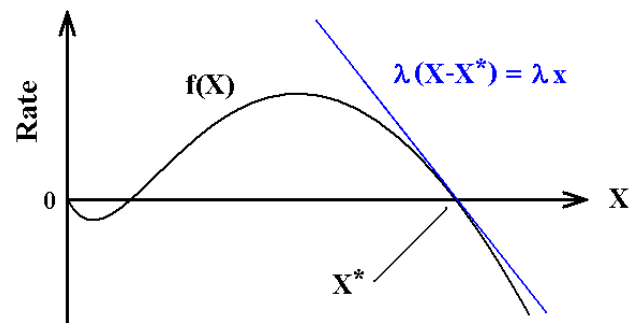


Figure 11. Linear approximation of nonlinear population growth near equilibrium.

4. The solution to Eq (13) is

$$x(t) = x_0 e^{\lambda t} \quad (14)$$

5. Hence the stability requirement, $\lambda < 0$, *i.e.*,

$$x(t) \rightarrow 0 \Leftrightarrow \lambda < 0 \quad (15)$$

6. For discrete systems, the corresponding result is

$$x_t = x_0 \mu^t \quad (16)$$

Hence the stability requirement,

$$-1 < \mu < 1 \quad (17)$$

J. Allee Effect.

1. Synergistic *population* growth at low N .
2. Consequence of
 - a. “Cooperation”: predator mobbing; pack hunting; extracellular polymeric substance (EPS) production.
 - b. Stochastic extinction of small populations.

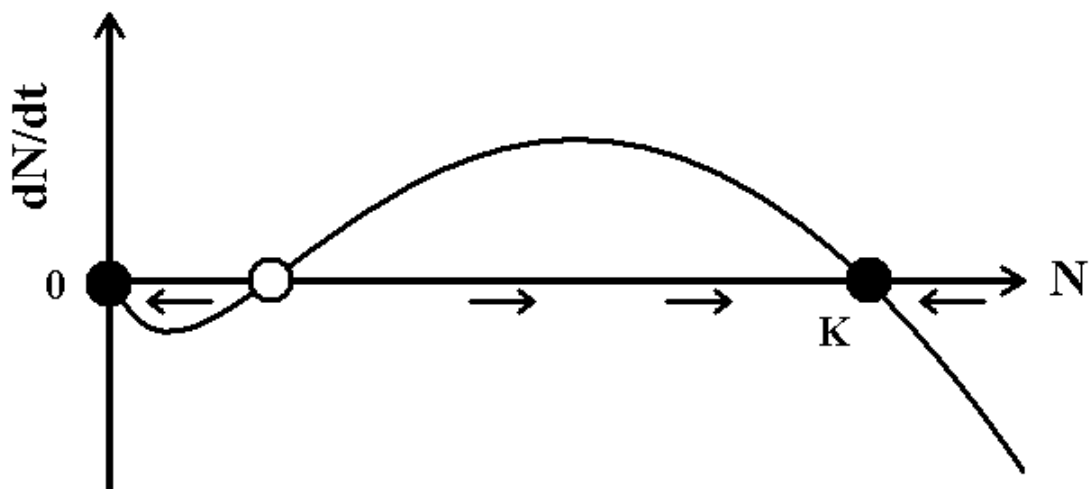


Figure 12. In the case of an Allee effect, $N = 0$ is stable, and there is an unstable equilibrium between it and $N = K$.

II. Harvesting

A. Proportional Removal.

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - hN \quad (18)$$

1. Here h is the harvesting rate, and $H = hN$, the number of individuals removed per unit time.

2. Assumes harvest rate proportional to N .

3. As before, there are two equilibria:

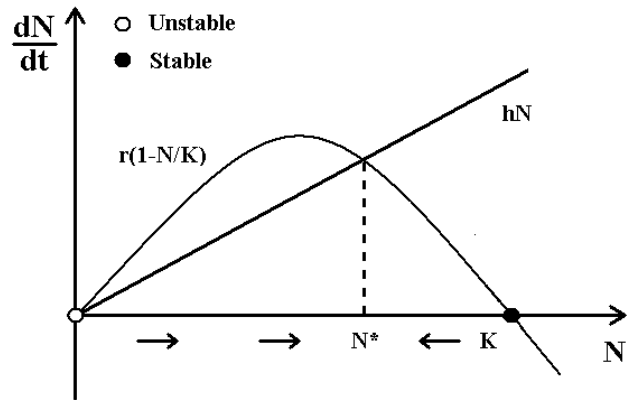


Figure 13. Logistic growth with proportional removal. Units of h are 1/time.

$$N^*(h) = \left(1 - \frac{h}{r} \right) K \quad (19)$$

(*non-trivial* equilibrium) and $N = 0$ (*trivial* equilibrium).

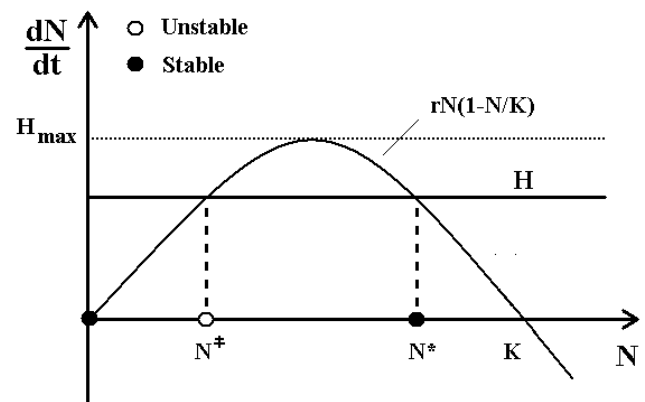
4. With $h < r$, $N = 0$ is unstable; and N^* , stable.

5. At $h = r$, the equilibria collide and there is an *exchange of stability* (*transcritical bifurcation*).

6. With $h > r$, N^* remains stable, but is now negative and therefore of no biological relevance.

B. Constant Removal.

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - H \quad (20)$$



1. From Figure 14, we see that there are two possibilities.

Figure 14. Logistic growth with constant removal. Units of H are individuals/time.

2. Case 1. $H < H_{max}$.

a. Two equilibria.

b. $0 < N^{\ddagger}$ (unstable) $< N^*$ (stable).

3. Case 2. $H > H_{max}$.

a. No equilibria.

b. Population \rightarrow extinct.

4. At $H = H_{max} = \frac{rK}{4}$, there is a *tangent bifurcation*.

a. $H = \text{const}$, is tangent to dN/dt absent harvesting.

b. Two equilibria that pop into existence

$$N^*, N^\ddagger = \frac{K}{2} \left[1 \pm \sqrt{1 - 4 \frac{H}{rK}} \right] \quad (21)$$

c. Note that

$$N^*(H_{max}) = N^\ddagger(H_{max}) = \frac{K}{2} \quad (22)$$

$$\left. \frac{dN}{dt} \right|_{\substack{H=0 \\ N=\frac{K}{2}}} = \frac{rK}{4}$$

5. With decreasing H , N^\ddagger moves left, while N^* moves right.

6. At $H = 0$ (smallest possible value), $N^\ddagger = 0$; $N^* = K$, and we recover the logistic without harvesting.

C. Maximum Sustainable Yield (MSY).

1. Plot stable and unstable equilibria vs. H (Figure 15).
2. $H > rK/4 \Rightarrow$ population collapse.

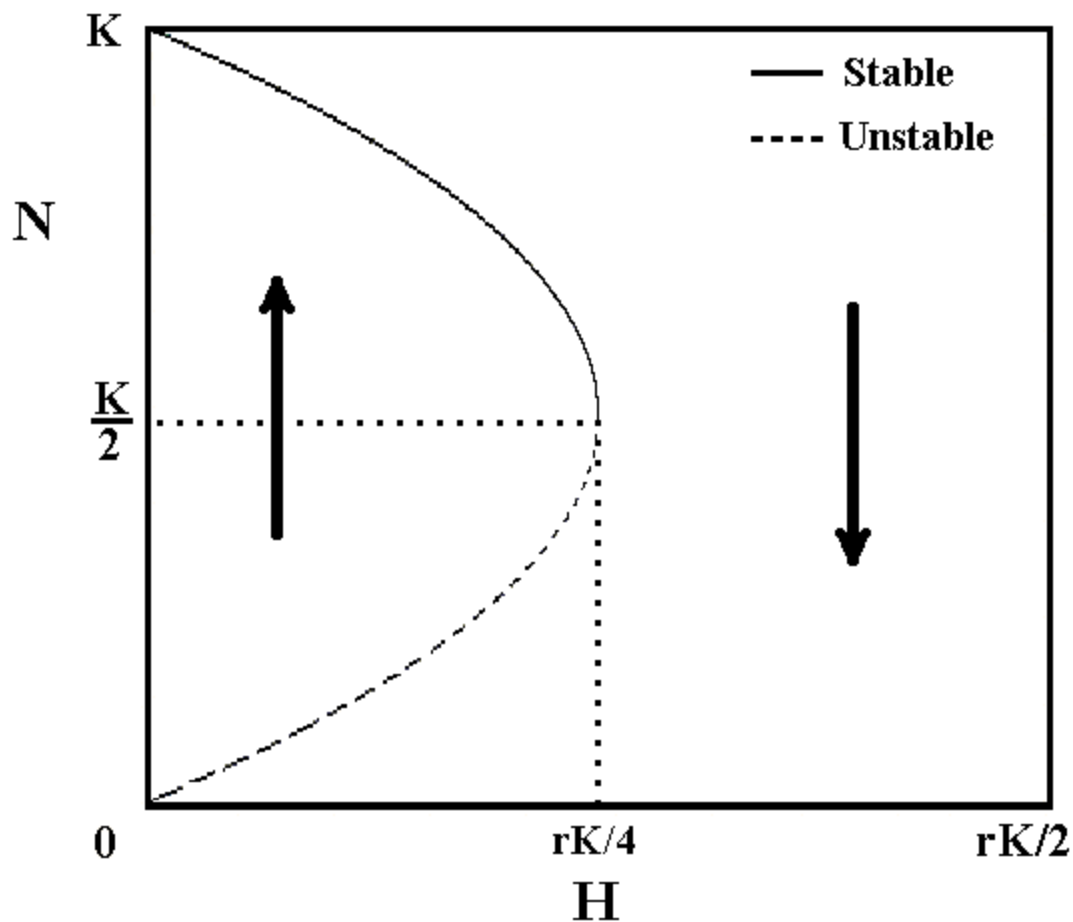


Figure 15. “Branches” of stable and unstable equilibria with constant harvesting. If $H > rK/4$, the population collapses. Arrows indicate change in N for fixed H .



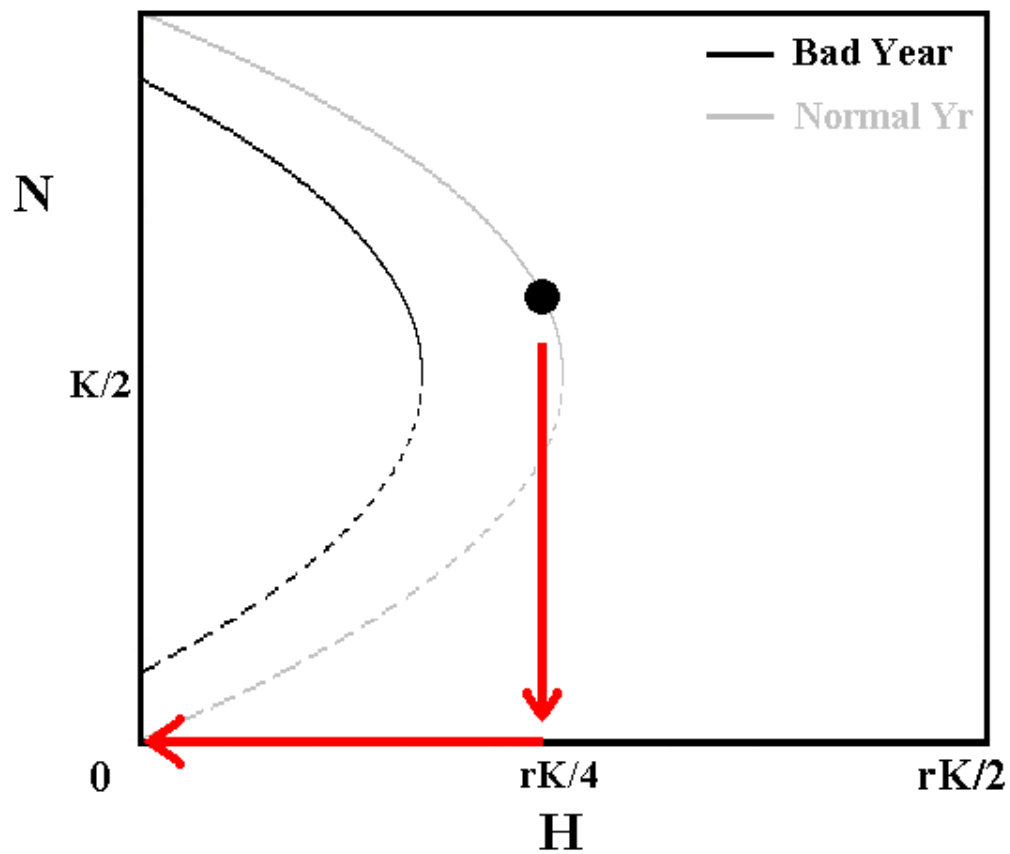
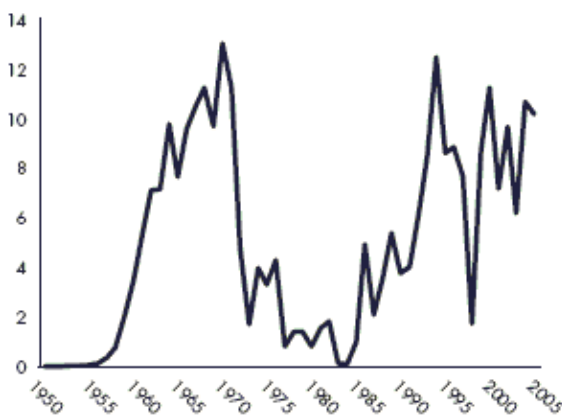


Figure 17. Harvesting below the MSY can lead to population collapse if the environment temporarily deteriorates.

5. Peruvian anchovy.

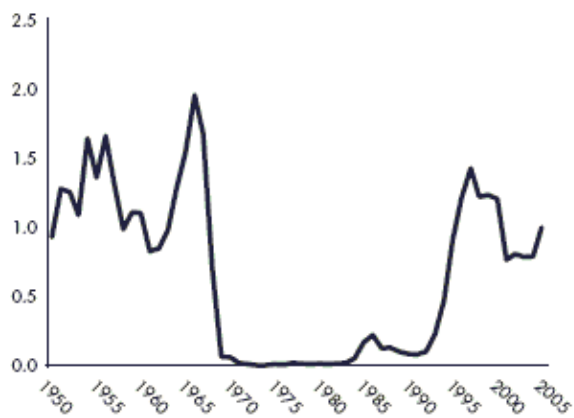
- a. From 1955-1970, fishing effort and harvest increased from $< 10^6$ to $>10^7$ metric tons.
- b. In 1972,
 - i. *El Niño* event reduced ocean productivity off the Peruvian coast.
 - ii. Anchovy population crashed (Figure 18) as one might predict from Figure 17.

Figure 4 **Catches of Peruvian anchovy**
Million tonnes



Source: FAO Fisheries Database

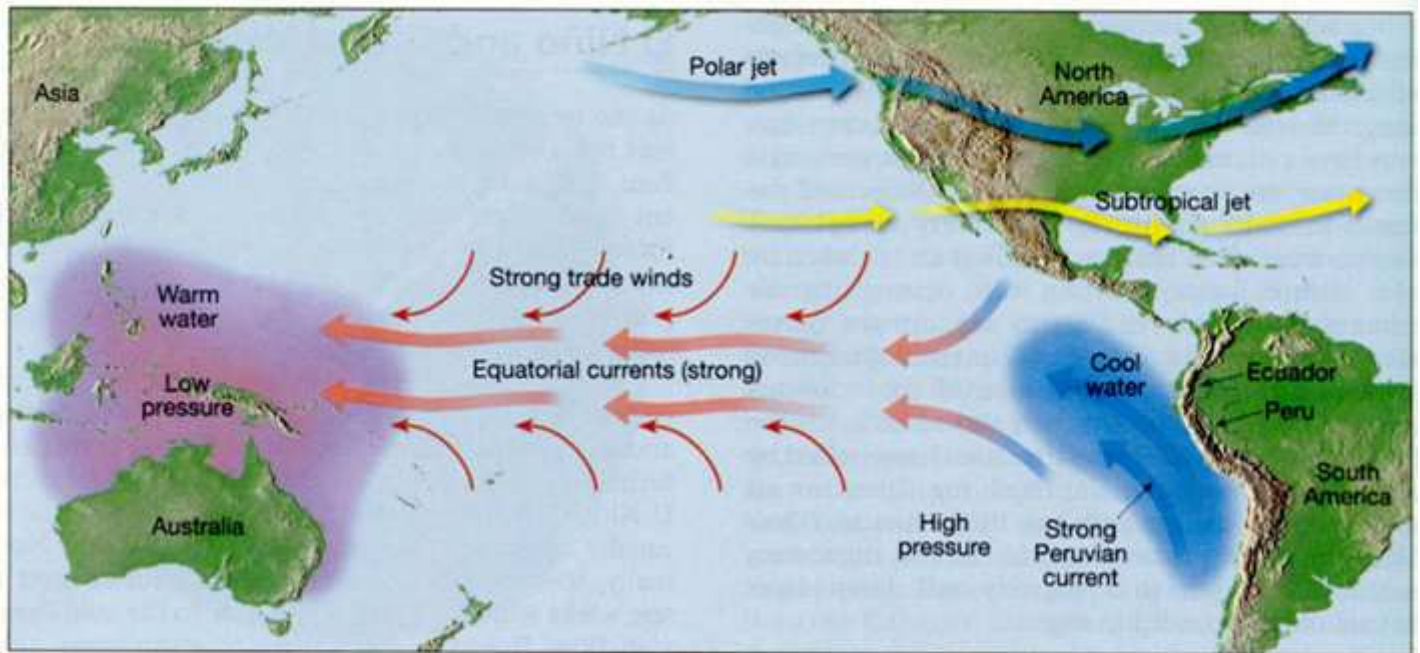
Figure 5 **Catches of Atlanto-Scandian herring**
Million tonnes



Sources: ICES, Northern Pelagic and Blue Whiting Working Group Report 2006, Table 3.5.2.1 and Institute of Marine Research, Bergen

Figure 18. Collapse and recovery of anchoveta (left) and herring (right). From Hannesson (2008).

- c. <http://www4.ncsu.edu/~dbeggles/education/synergy/anchovy/anchovy.html> gives details about the anchovy fishery. See also Hannesson (2008).
- d. <http://www.aviso.oceanobs.com/en/applications/climate/el-nino/what-is-el-ninola-nina/index.html> gives details about ENSO (*El Niño* Southern Oscillation).



Normally, the trade winds and strong equatorial currents flow toward the west. At the same time, an intense Peruvian current causes upwelling of cold water along the west coast of South America.

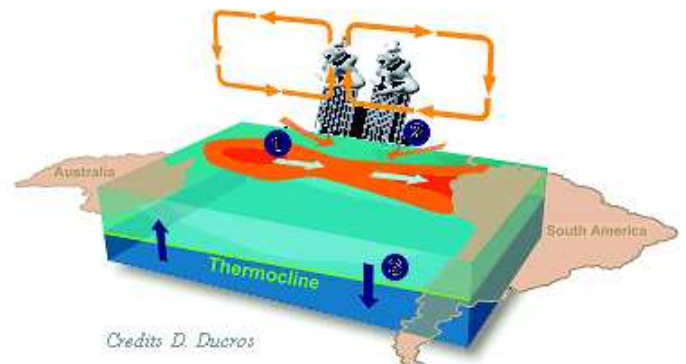
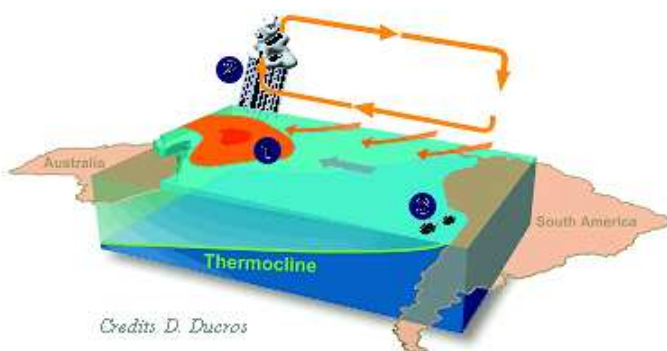


Figure 19. Top. Normal circulation in the southern Pacific. Bottom. Changing depth of the thermocline in normal (left) and *El Niño* (right) years. *La Niña* (not shown) is an intensification of the normal pattern. Both promote upwelling off the Peruvian coast and are thus favorable for anchovy. For additional information, follow the preceding links.

D. Hysteresis Loop – H fast. N slow.

1. Now add immigration, $I > 0$. Eqs 11 and 12 become

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right) - H + I \quad (23)$$

$$N^*, N^\ddagger = \frac{K \pm \sqrt{K^2 - 4 \frac{K(H - I)}{r}}}{2} \quad (24)$$

2. Assumes *rapid* population response (N a *fast* variable) to changes in H – *separation of time scales* permits model simplification.

3. Result is the *hysteresis loop* shown in Figure 20.

a. Fast variable slowly tracks changing equilibria, *i.e.*,

$$N(t) \approx N^*(H(t)). \quad (25)$$

b. Hysteresis a common consequence of non-linearity in both physical and biological systems.

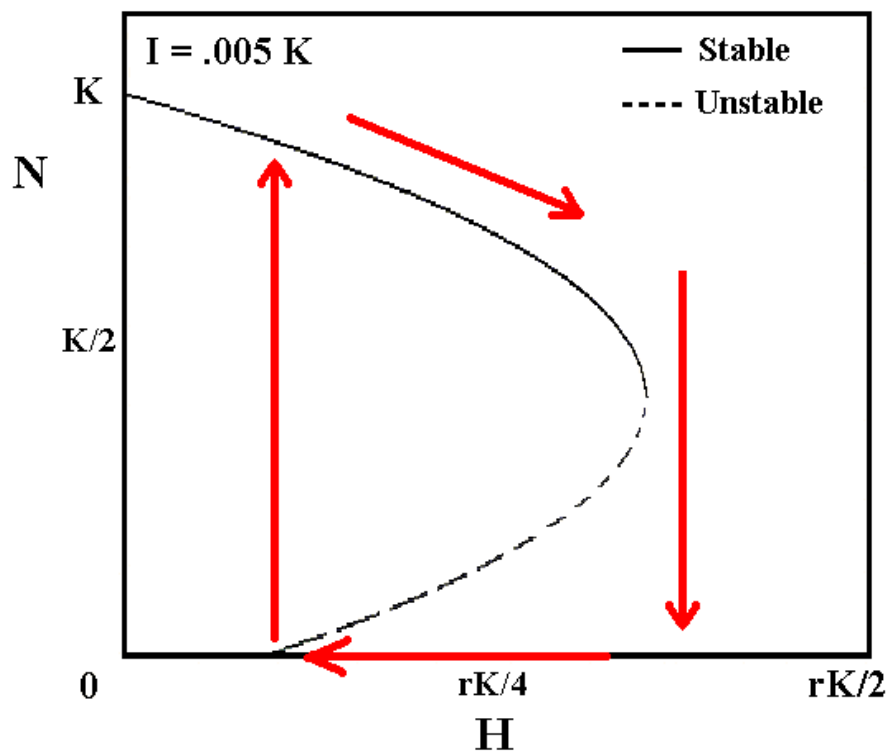


Figure 20. With small constant immigration and slowly changing H , $N(t)$ recovers when $H < I$.

III. Time Delays.

A. Gotelli discusses the delay logistic equation:

$$\frac{dN}{dt} = rN \left(1 - \frac{N(t - \tau)}{K} \right) \quad (26)$$

1. With increasing time delay, τ , stable equilibrium gives way to stable cycles.
2. If we replace r in Eq 20 with $(b - d)$, we see that the logistic is “special” in that both are equally affected by the delay.
3. Relaxing this assumption \Rightarrow a greater diversity of dynamics.

B. Mackey-Glass equation (white blood cell production) an example.

$$\frac{dx}{dt} = b \frac{x(t - \tau)}{1 + x(t - \tau)^z} - dx \quad (27)$$

1. With increasing τ , stable equilibrium yields to dynamics of increasing complexity (Figure 21).

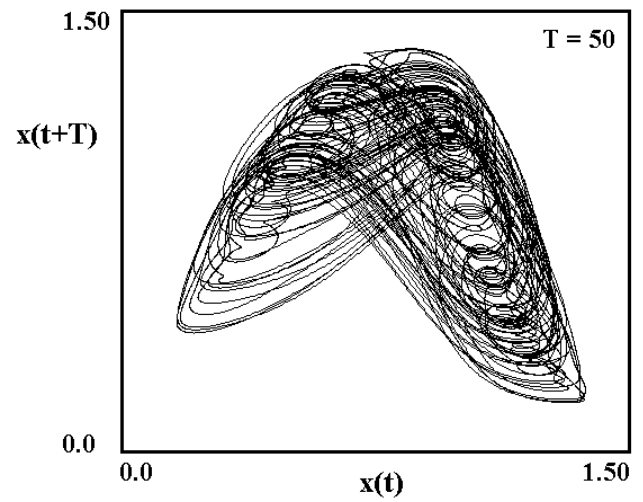
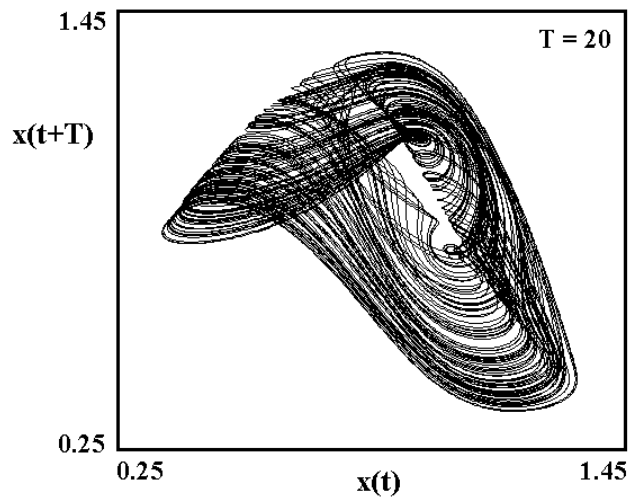
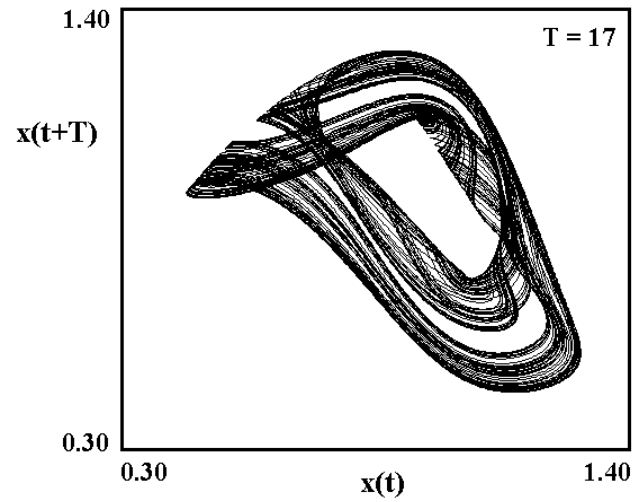
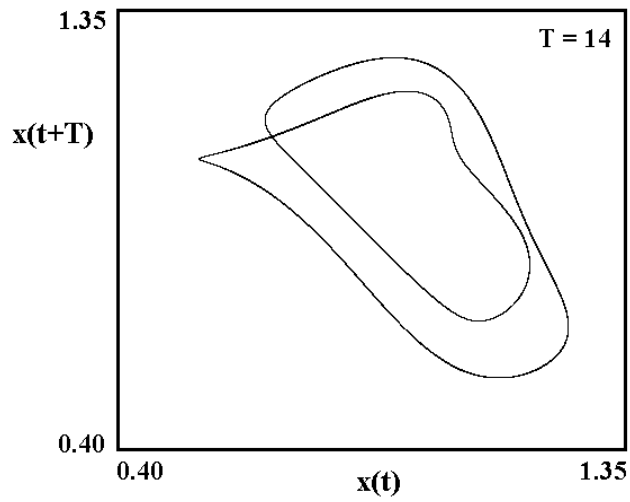


Figure 21. Non-equilibrium dynamics in Equation 18 with $z = 10$, $b = 0.2$, and $d = 0.1$ for different values of the time delay τ . With increasing τ , the dynamics become more complex.

V. Discrete Logistic.

A. Census population at generational intervals. We study

$$X_{t+1} = r'X_t(1 - X_t) \quad (28)$$

1. In terms of Gotelli's Eq 2.3,

$$X_t = \frac{rN_t}{(1+r)K}; \quad r' = 1 + r \quad (29)$$

2. Eq 26 is “dimensionless” – neither X nor r' has units.

3. “Non-dimensionalizing”

- a. Eliminates parameters.
- b. Tells you what's important.

4. Henceforth we write the discrete logistic as

$$X_{t+1} = rX_t(1 - X_t) \quad (29)$$

and **remember (!!!)** that r has been re-defined.

B. Equilibria.

$$\begin{aligned} X^0 &= 0 \text{ (trivial equilibrium);} \\ X^* &= 1 - 1/r \text{ (non-trivial equilibrium).} \end{aligned} \tag{30}$$

C. Stability of X^0 .

1. Compute (Eq 9b) the value

$$\mu = \left. \frac{d}{dX} X' \right|_{X=0} = r(1 - 2X)|_{X=0} = r \tag{32}$$

2. X^0 stable $\Leftrightarrow -1 < r < 1$ – alternatively, $|r| < 1$.

D. Stability of X^* .

1.

$$\mu = \left. \frac{d}{dX} X' \right|_{X=X^*} = r(1 - 2X)|_{X=X^*} = 2 - r \tag{33}$$

2. X^* stable $\Leftrightarrow 1 < r < 3$

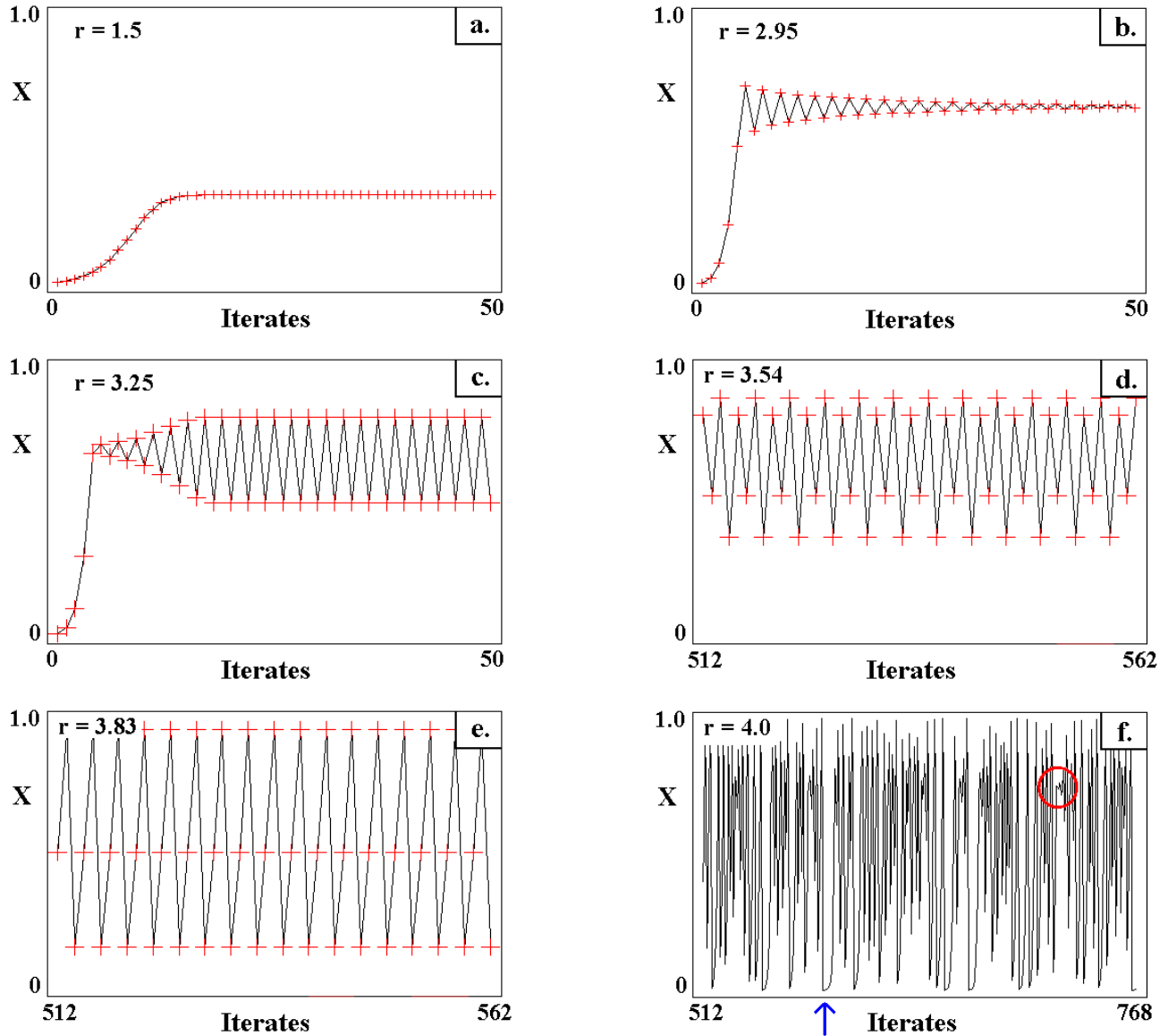


Figure 22. For $1 < r < 3$, the discrete logistic has stable equilibrium, $X^* = 1 - 1/r$ to which solutions initialized on $(0,1)$ converge. For $r < 1$, the approach to equilibrium is direct (a); for $2 < r < 3$, via damped oscillations (b). At $r = 2$, there is the first of a series of period-doubling (PD) bifurcations (c, d) that accumulate at $r \approx 3.57$. There follows a mix of periodic and chaotic behavior. Shown here is a period-three cycle (e) and a chaotic solution (f). The latter is filled with equilibria and cycles, but they are all unstable. The blue arrow indicates a point on the solution close to $X = 0$; the red circle, a point close to $X^* = 1 - 1/r = .75$.

E. Cobwebbing is a graphical technique for solving equations like the discrete logistic.

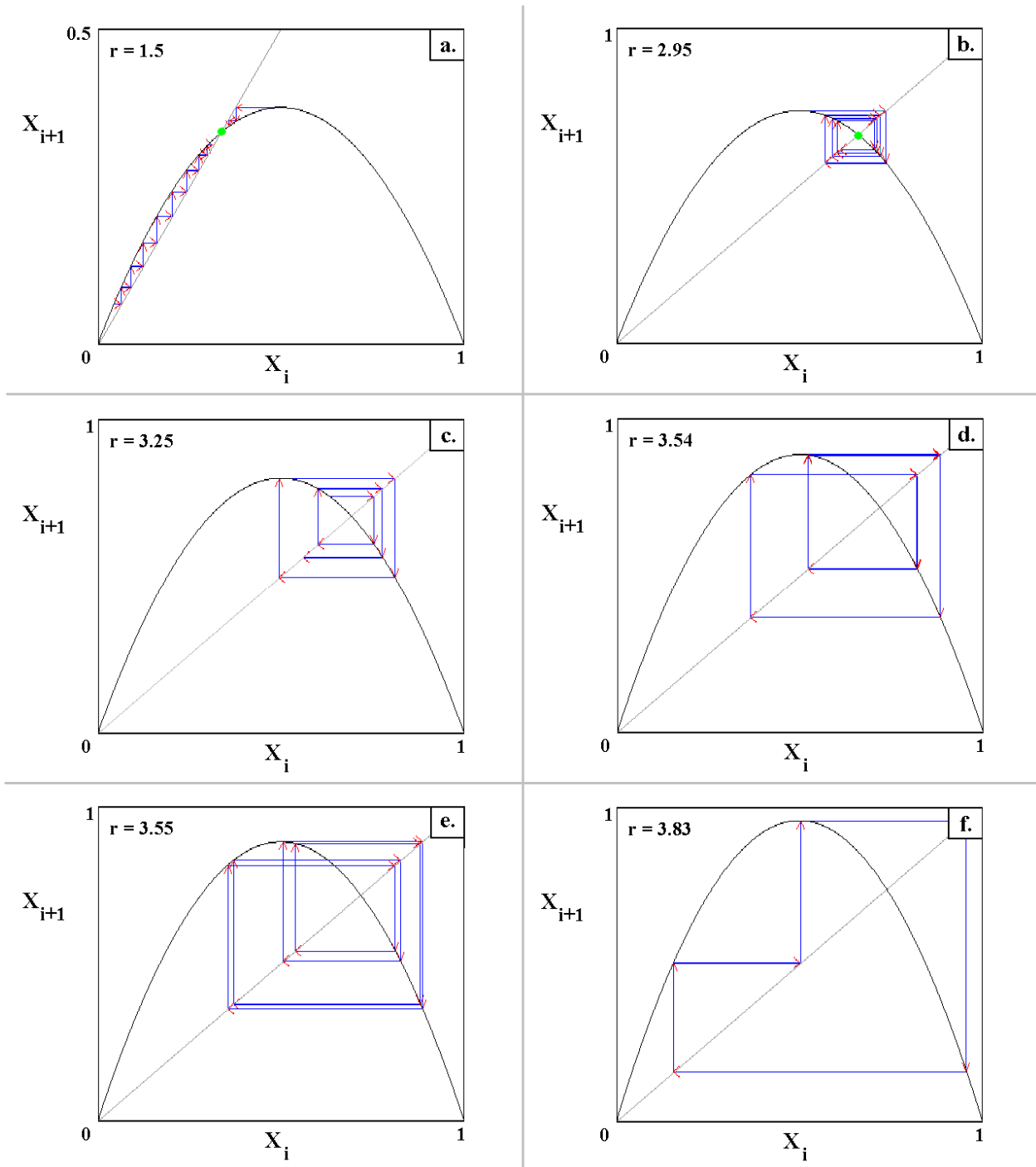


Figure 24. Iterating the discrete logistic graphically.

F. One can show (but we will not) that

1. At $r = 3$, a stable two-point cycle comes into existence.
2. With increasing values of r , the 2-cycle loses stability, and is replaced by a 4-cycle; the 4-cycle, by an 8-cycle, *etc.*, until at $r \approx 3.57$, the period becomes infinite.
3. For higher r values there is a complex mix of periodic and chaotic behavior.
 - a. Chaotic motions manifest **sensitivity to initial conditions** (SIC).
 - b. SIC \Rightarrow unpredictability.
 - c. Nearby points diverge so that long-term, the only thing that can be predicted is a probability distribution (Figures 25).

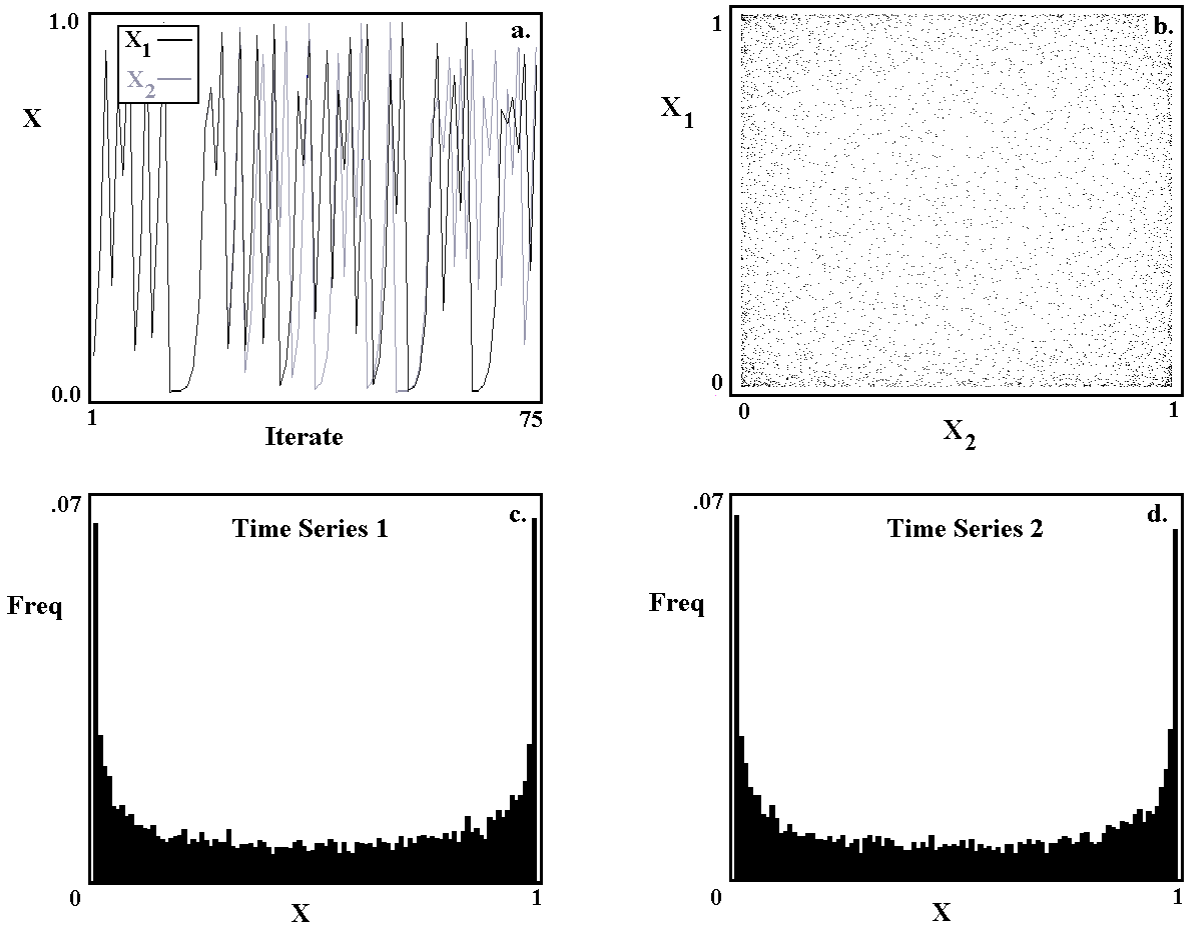


Figure 25. Sensitivity to initial conditions in the logistic map with $r = 4$. a. Time series based at initial points X_0 and $X_0 + \epsilon$, with $\epsilon = 10^{-9}$, superimposed. After a surprisingly short number of iterations, the time series diverge. b. 10,000 points from the two time series plotted against each other. c. Frequency distribution for values of X realized in the first time series. d. Frequency distribution for the second time series.

VI. Real Populations.

A. Hassell, Lawton and May suggested complex dynamics rare in nature (Figure 26).

B. \Rightarrow population fluctuations environmentally induced.

C. But – many populations manifest sustained, more or less regular fluctuations.

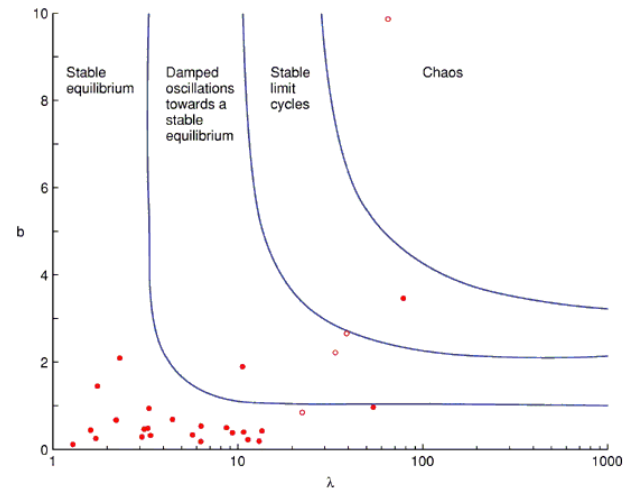


Figure 26. Dynamics of laboratory and field obtained by fitting $N_{t+1} = \lambda N_t(1 + aN_t)^{-\beta}$.

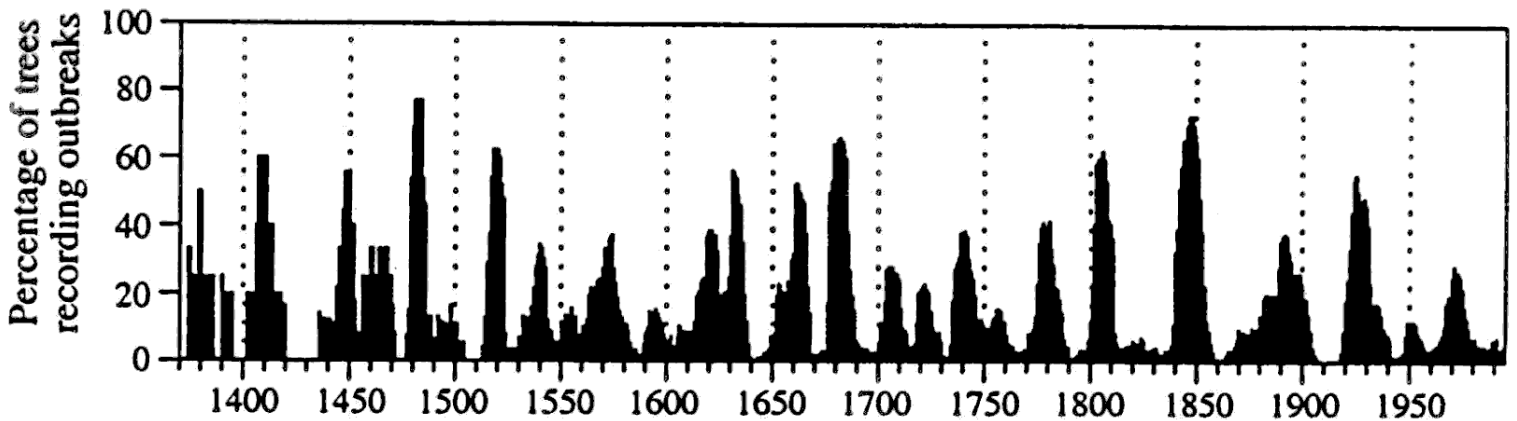
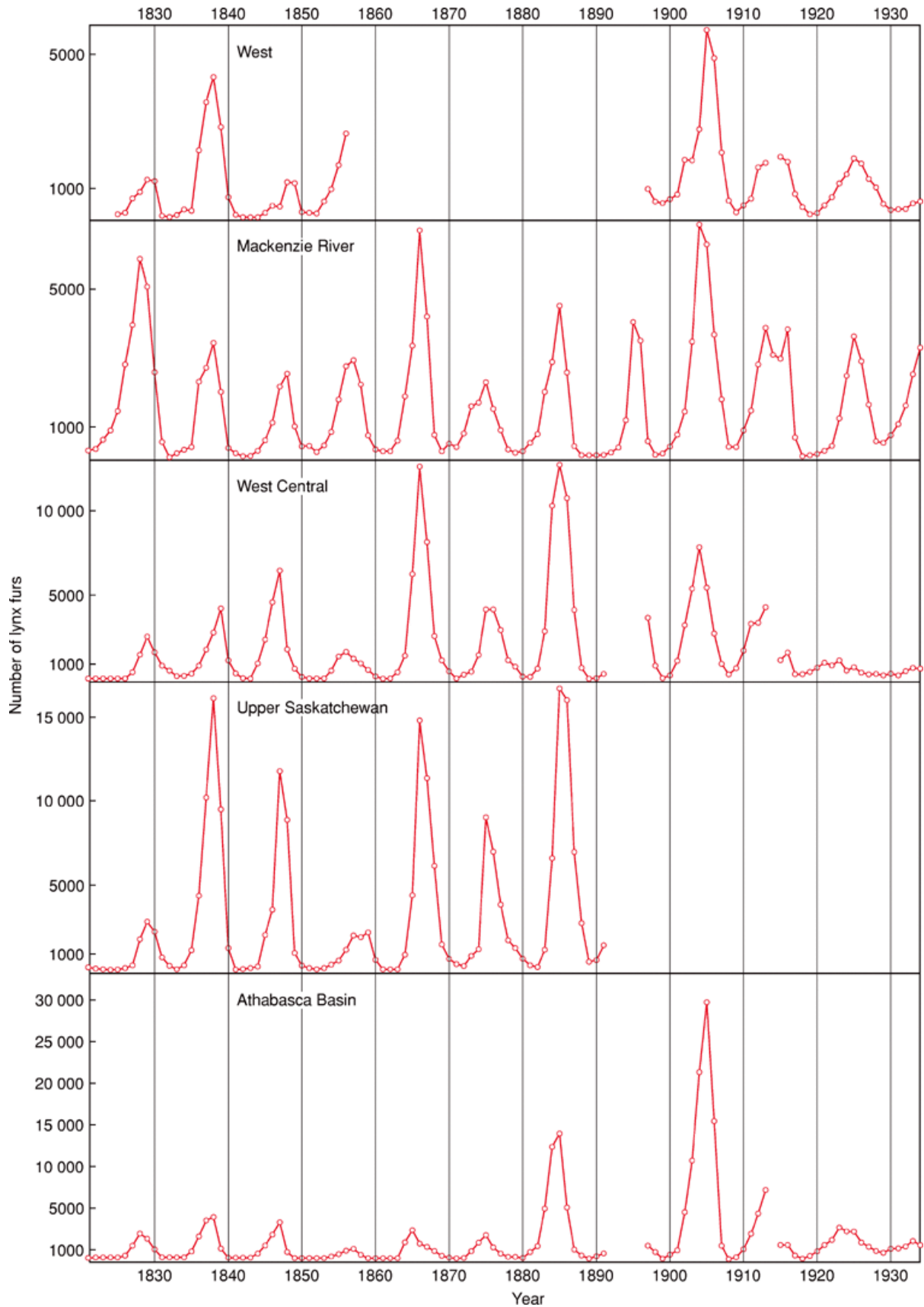


Figure 27 (above). Six hundred years of *Pandora* moth abundance reconstructed from tree rings.

Figure 28 (next page). Canadian lynx (*Lynx canadensis*) fur returns from various regions in Canada manifest cross-continental synchrony and an approximate 10-year periodicity. From Gillman (2001).



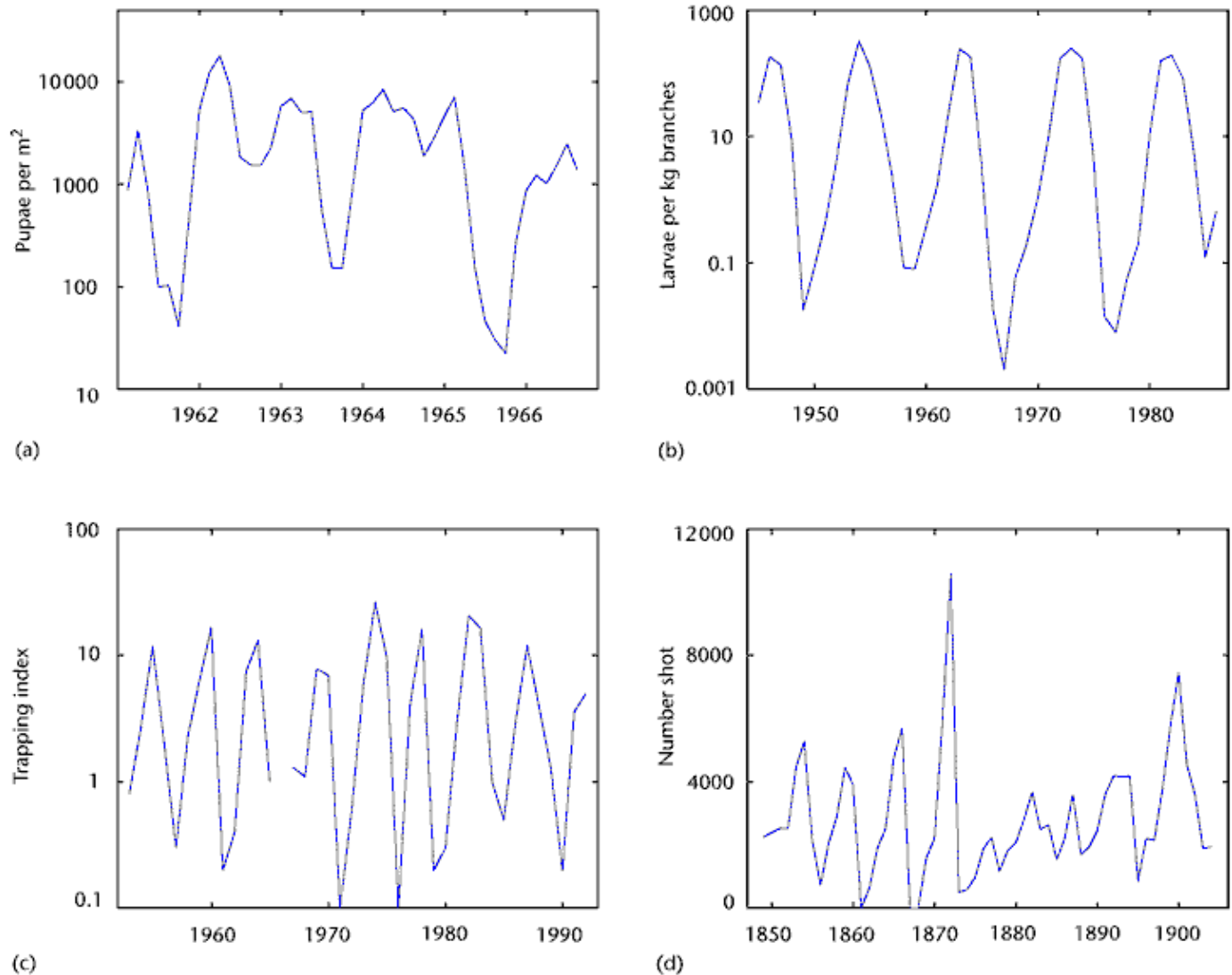


Figure 29. Fluctuating populations in nature. (a) Coffee leaf-miners (*Leucoptera* spp.) in Tanzania. (b) Larch bud-moth (*Zeiraphera diniana*) in Switzerland. (c) Voles (*Microtus* and *Clethrionomys*) in Finland. (d) Red grouse (*Lagopus lagopus scotius*) in Scotland. From Kendall (2001)

1. In the cases of *Pandora* and the *Lynx*, especially, it is difficult to imagine that these are responses to environment.

D. Why HLM conclusion suspect.

1. In nature, dynamics are *always* continuous.
 - a. The insects are there (as eggs, larvae, pupae) even if we don't count them.
 - b. So difference equations not really appropriate.
2. Populations in nature *never* exist in isolation – they *always* interact with other populations / species.
3. Logistic-like dynamics can sometimes be extracted from multi-species continuous models.
[\(<http://bill.srn.arizona.edu/demos/rossler/rossler2.html>\)](http://bill.srn.arizona.edu/demos/rossler/rossler2.html)
 - a. If population dynamics modeled as single-species difference equations, the parameter(s) determined by the entire system – not reproduction and survival of single species at a fixed point in time.
 - b. Estimating r from reproduction / survival of one species at fixed point in time a prescription for error.