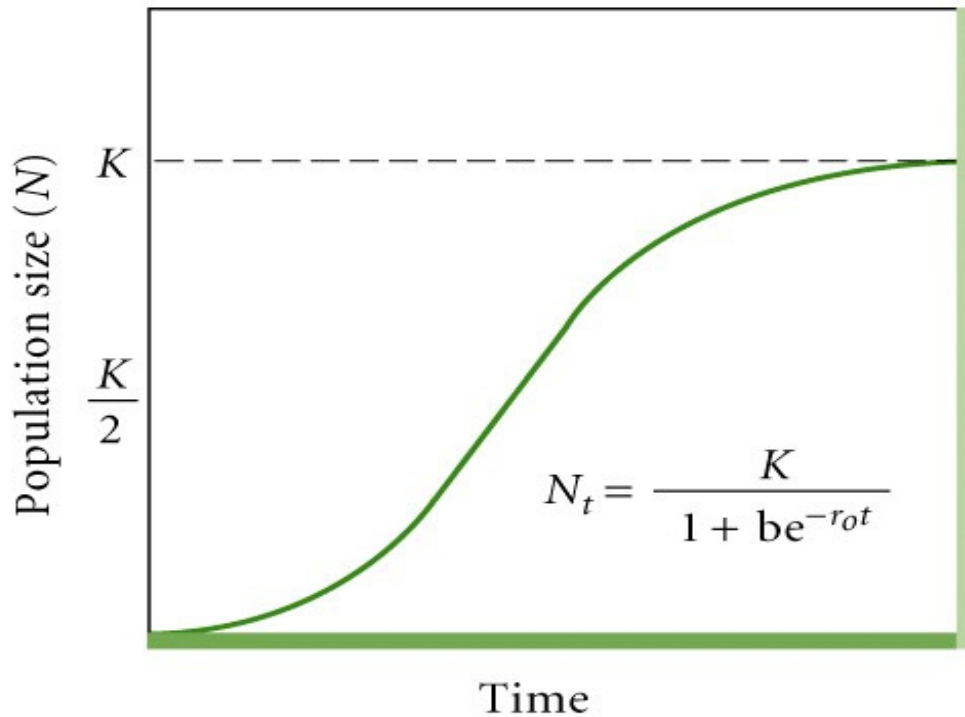


**Logistic Growth:** Quadratic, No Time Delay, K Constant



$$b = [K - N(0)]/N(0)$$

Logistic Population Growth

Simple Assumption: Instantaneous Feedback

$$dN(t)/dt = F[N(t)] N(t)$$

Each Individual Added Immediately Reduces  $F[N(t)]$

# Australian Sheep: maximal growth rate 25 yrs

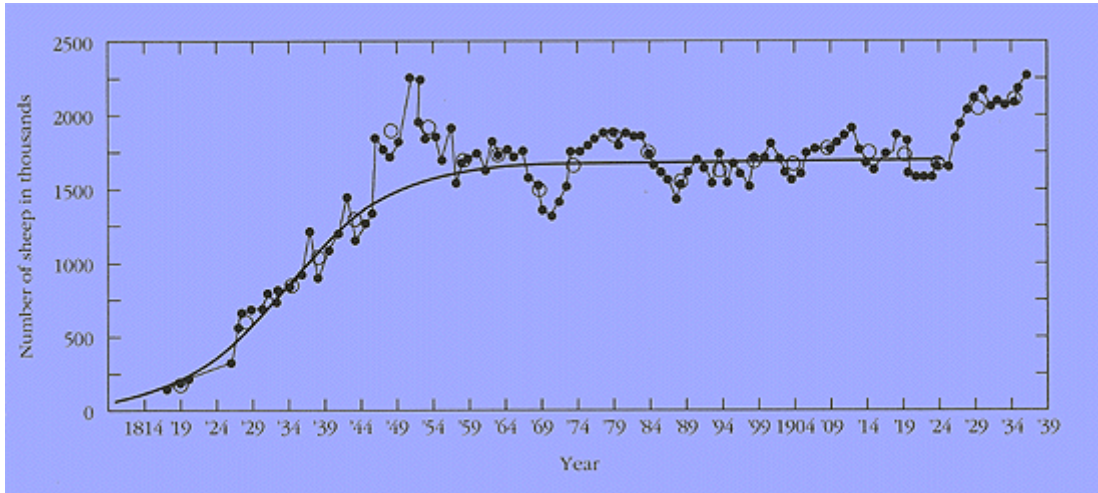
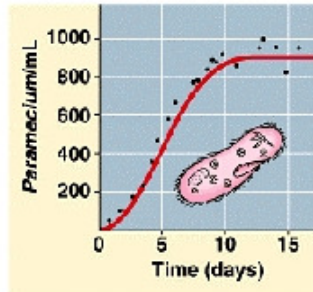
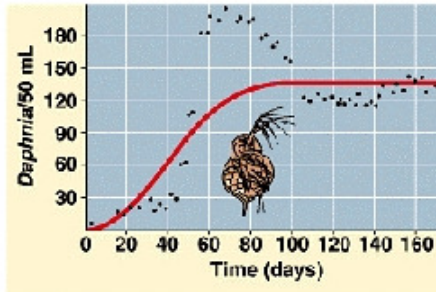


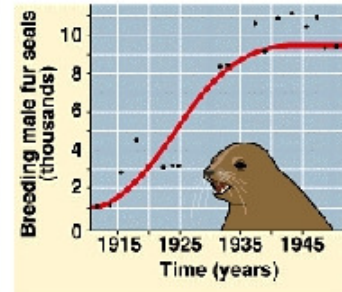
Figure 52.15 Examples of logistic population growth



(a) A *Paramecium* population in laboratory culture



(b) A *Daphnia* population in laboratory culture



(c) A fur seal (*Callorhinus ursinus*) population on St. Paul Island, Alaska

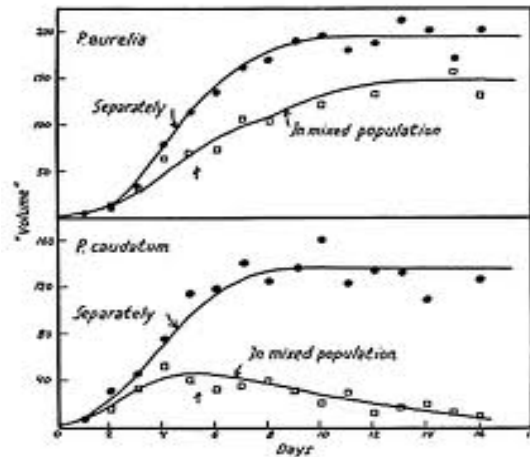
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Protozoan, small metazoan & large mammal:

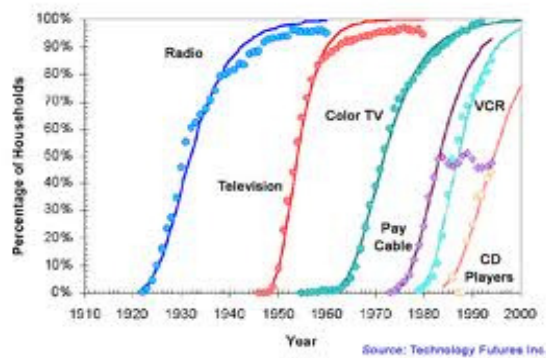
Logistic growth (app.), Increasing time to max  $dN/dt$

Gause 1930's: *Paramecia* spp.



Sigmoid growth: arises from many dynamics

Ecology, chemistry, epidemiology, sociology, technology



How might logistic growth's assumptions fail biologically?

Density-dependent feedback delayed during maturation

Age (Time to Maturity), Size May *Delay*

Newborn Individual's Impact on Per-Capitum Growth

Alternative Assumption: Time Delay, Lagged Logistic

$$dN(t)/dt = F[N(t - \tau)] N(t)$$

$\tau$  Time Delay

At time  $t$ , Density Dependence Responds to

Population Size at time  $(t - \tau)$ ; i.e.  $\tau$  Time Units *Earlier*

**Population Can Grow Beyond  $K$**

**Time Lag May Destabilize  $K$**

## Standard Logistic Modified with Time Delay

$$dN(t)/dt = rN(t) \left[ 1 - \frac{N(t-\tau)}{K} \right]$$

$K$ : Carrying Capacity, Constant

$r$ : Intrinsic Rate of Increase ~

Individual Growth Rate When Rare

$\tau$ : Time Delay

Population Reproduction:

Responds to Density  $\tau$  Time Units Earlier

Predict Population Behavior?

Key: Delay  $\div$  “Response Time” =  $r\tau$

$\tau \rightarrow 0$ , Standard Stability Condition ( $r > 0$ )

$\tau > 0$ :

$r\tau$  small enough ( $r\tau < e^{-1} = 0.368$ ):

Standard Increase to Stable  $K$

$r\tau$  “intermediate” ( $e^{-1} = 0.368 < r\tau < 1.571 = \pi/2$ ):

Damped Oscillations;  $K$  stable

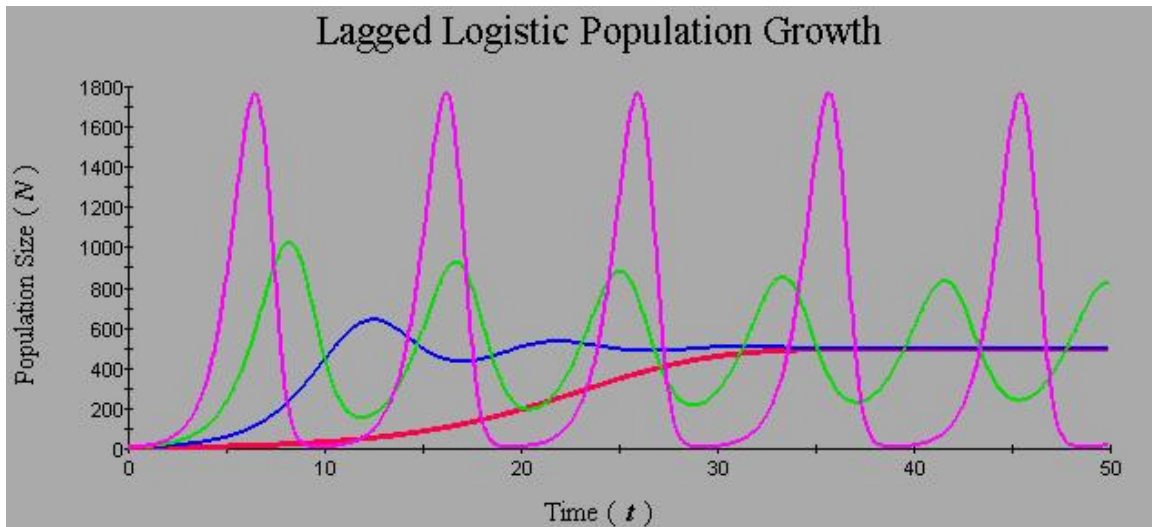
$r\tau$  large enough ( $r\tau > 1.57 = \pi/2$ ):

Stable Limit Cycles;  $K$  Unstable: Focus of Cycles

Fix time Lag ( $\tau = 2$ )

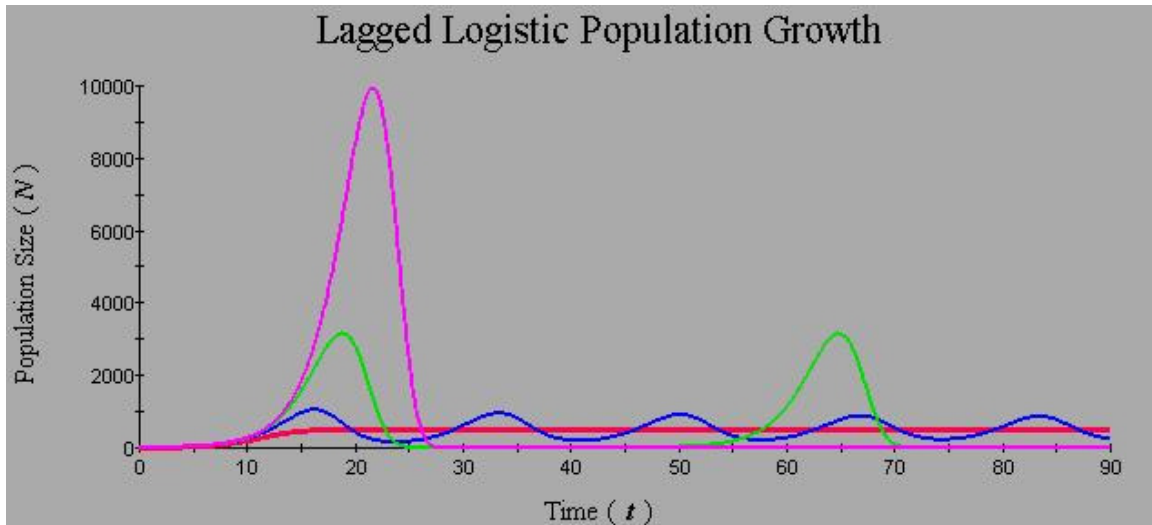
$K = 500$

Increase  $r$ , Population Responds “Too Fast”



Greater  $r$ , Larger Population Fluctuation

Fix  $r$ , Increase Time Lag



Greater Lag, Larger Fluctuation, Lower Frequency

Period of Stable Limit Cycle =  $4\tau$  (Independently of  $r$ )

Frequency =  $1/\text{Period}$

**Lesson:** **Time delay** in density-dependent population regulation may **destabilize** population growth, and increase **dynamic complexity**.