

# Population Regulation

## I. Background

What determines the number and kinds of animals and plants in an area?

Why don't animals and plants fulfill their potential to grow exponentially?

What does population regulation mean?

Can we detect density-dependent regulation in real populations? How frequent?

# Population Regulation

## I. Background

### Schools of thought

- Density related factors (facultative = density dependent)
- Density-dependent factors of secondary or no importance, density independent factors and time primary
- Both important
- Genetic factors control dynamics
- Spatially structured dynamics (source-sink, metapopulation, ‘spreading the risk’, etc)

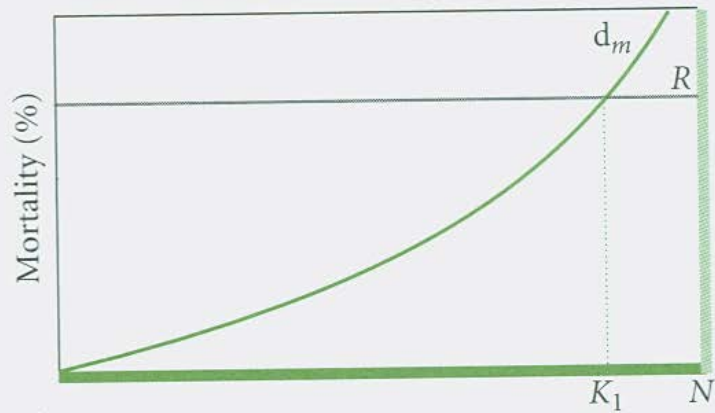
# Theories – Regulation in natural populations

- Maltus (1798): ‘Essay on Principles of Population.’ Exponential pop growth with ultimate resource limits
- Darwin (1886): invoked Malthus as mechanism for natural selection
- Moebius (1877): natural enemies
- Howard and Fiske (1911): DD vs DI factors make up ‘environment’
- Nicholson (1933): DD = food availability, intraspecific competition (blowflies)
- Elton (1949): Intraspecific competition (Voles, lemmings)
- Lack (1954): Intraspecific & interspecific competition birds
- Adrewartha and Birch (1954): density independent – run out of time to fulfill potential (r) (thrips)

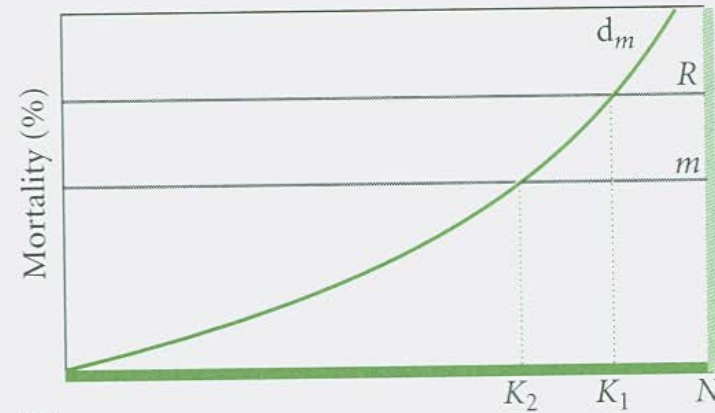
# Population Regulation

- Milne (1957): imperfect density dependence
- Chitty (1960): self regulation through genetically induced changes in individual vitality; select for more/less vigorous individuals at different densities
- Pimental (1961): regulation by coevolution of predator and prey; genetic feedback for Nicholsonian response
- Wynne-Edwards (1962): animal dispersion and social behavior leads to self-regulating populations
- Dempster (1983): regulation with floors and ceilings
- Strong (1986): density vague regulation; density independent fluctuation except for extremes (same as density dependence with non-linearities and 'noise')

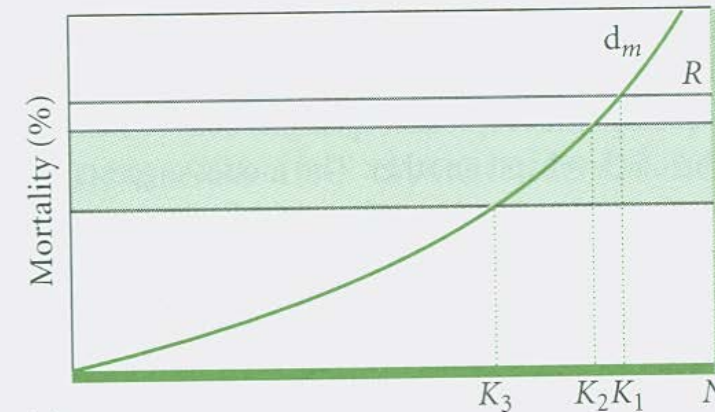
# Incorporating multiple factors into regulation



(a)



(b)



(c)

## Key

$R$  = reproduction rate

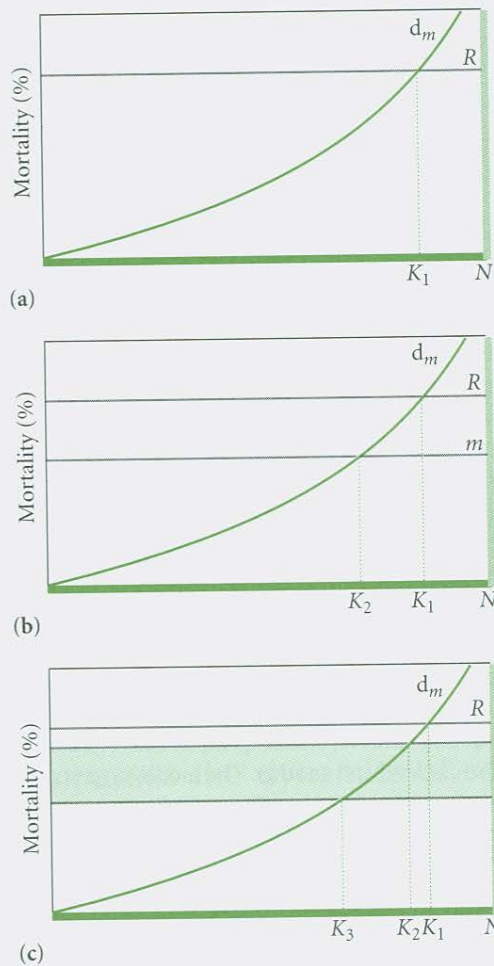
$d_m$  = d-d mortality factor

$m$  = d-i mortality factor

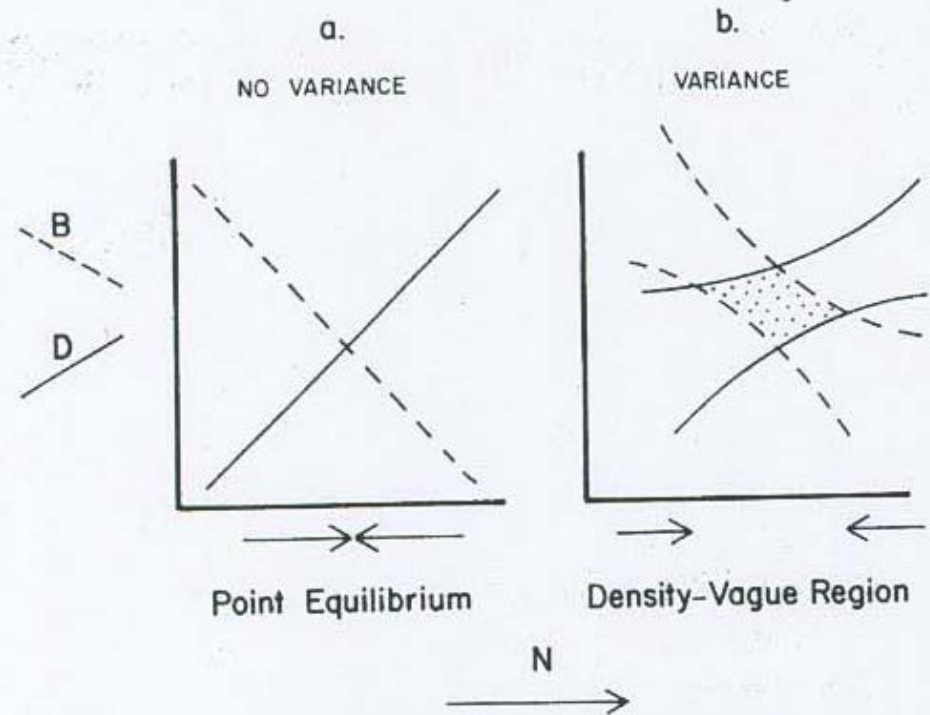
$K_{1,2,3}$  = Carrying capacities

Green shade = env stochasticity

# Incorporating Stochasticity Into Regulation



**FIGURE 16-19** Possible interactions between density-dependent and density-independent mortality factors. (a) A population with a constant rate of reproduction,  $R$ , and a density-dependent mortality rate,  $d_m$ , showing an equilibrium point at  $K_1$ . (b) A similar population having both a density-dependent mortality rate and a density-independent mortality factor,  $m$ . The presence of the density-independent factor lowers the population equilibrium density to  $K_2$ . (c) A population in which the density-independent mortality factor fluctuates (within the green shaded area) in response to environmental stochasticity, creating a situation in which the equilibrium density fluctuates between  $K_2$  and  $K_3$ . (After Sinclair and Pech 1996.)



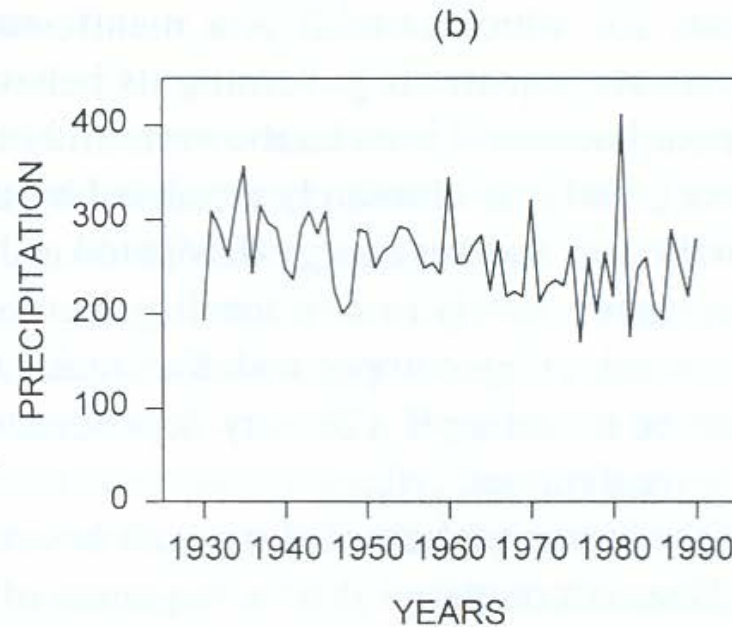
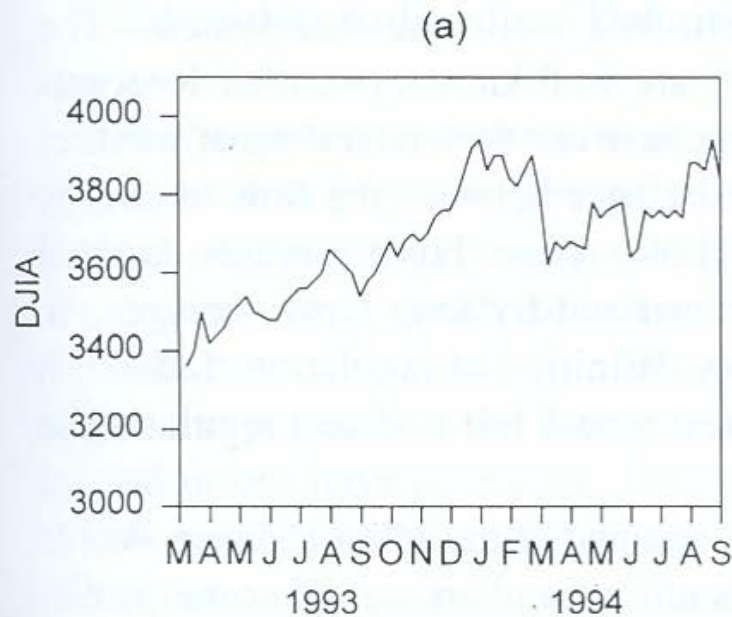
**Fig. 2.** Per-capita birth and death rates as a function of population density in the simplest of models. On the left (a) with no variance, the intersections of the rates mark an equilibrium point for density. On the right (b) the functions have variances, which create a medial region of indeterminacy for population density. Prediction intervals shown for b. Figure from ref. 23. Copyright © 1986 by Harper and Row Publishers, Inc.

# Population Regulation

## Definitions

A. Population regulation = a long-term stationary probability distribution of population densities (some mean density around which population size fluctuates)....

Variance is bounded, non-regulated time series has increasing variance over time. Also, unregulated time series not characterized by mean population size.



**Figure 1.** (a) Fluctuations in the Dow Jones Industrial Average (DJIA) index over 18 months. (b) Fluctuation pattern of annual rainfall (in cm) over 67 years on Barro Colorado Island, Panama. (Data from Wolda and Dennis, 1993.)

**DJIA:** Note mean goes up; not a stationary system though fluctuations are governed by ‘endogenous’ factors (can go too high [=overvalued stocks] and will self regulate back down



1. Random walk is a special case of unregulated time series. Birth = Death, so no long term increase or decrease, BUT no stationary probability distribution (i.e., variance increases with time).

$$N_{t+1} = \lambda N_t \quad \text{substitute to get} \quad N_{t+1} = \varepsilon_t N_t$$

Take logs to get:

$$\ln N_{t+1} = \ln N_t + \varepsilon_t$$

$$R_t = \varepsilon_t$$

[Note: where  $R_t = \ln N_{t+1} - \ln N_t$ ]

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- Note: unregulated does not equal random... exponential growth or decline is unregulated but not random.
- Note: random walk described as path a drunk follows as when walking across a parking lot... each set of steps proceeds in a random direction, but starts at the end of the last set.

2. Random number string is not a random walk:  $N_{t+1} = \varepsilon_t$

# Other Definitions and issues

1. Regulated population is one that returns to an equilibrium density after departure

\*Requires a stable point equilibrium as from Lotka-Volterra or discrete logistic models... ignores role of exogenous environmental variables on stable point and 'noise'

2. Regulated population is one that fluctuates within limits

\*Implies floors and ceilings, probability distribution declines to zero at extremes

\*Equilibrium point in non-linear systems called an 'attractor' = a stationary probability distribution of population density (equilibrium not a point, but a cloud of points)

[Geek speak: attractor is a compact set that attracts initial conditions from region around it; a strange attractor is special case that leads to non-repeating dynamics called chaos]

# Other Definitions and issues

## 3. Stochastic boundedness (Chesson 78, 82)

\*Probability of persistence... lower bound of density; Not a stationary probability distribution

## 4. Finite population size and spatial scale

\*Traditional analyses consider population scale as infinite (extinction is local), finite population scale shifts focus to persistence given fluctuations (Chesson 82)

## 5. Temporal scale of environmental fluctuations

\*Issue is ratio of generation time to period of fluctuations

Scales: < 1 year, model as stochastic  $\varepsilon_t$ ; decadal, may yield non-stationarity (gradual trends); century or more, too long to be important for most data sets (10-30 years)

# Alternative Definitions

**Regulation** = action of factors that function in a density-dependent manner to create an equilibrium density (one that is regained following a perturbation)

**Limitation** = the extent to which a population's per capita growth rate is depressed by the action of a particular factor (e.g., resource availability or predation risk)

**Control** = factors that set the equilibrium at a particular density; need not be density dependent

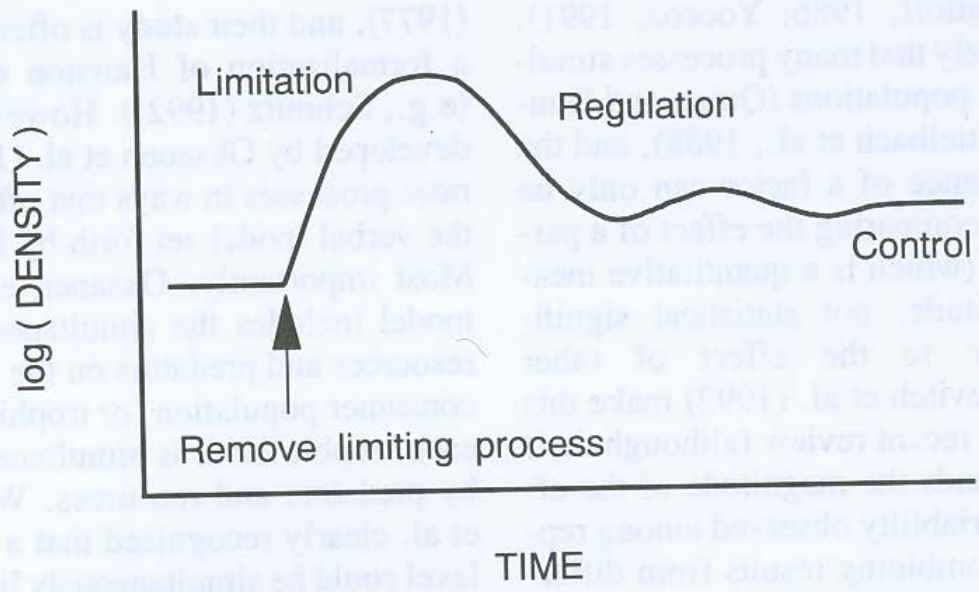


Figure 12.1. Graphical illustration of *limitation*, *regulation*, and *control*. Preceding a perturbation, the idealized system is at equilibrium and the density (measured as numbers or biomass per unit area) of the focal population (or trophic level) is constant. At the point of the perturbation (indicated by the arrow and representing, for example, the removal of predators or the addition of resources), the growth of the focal population increases. This increased growth rate results in an increase in density, but the growth rate eventually decreases due to feedbacks within the system (e.g., due to reductions in other resources or increases in other sources of mortality). The feedbacks arise from the existence of an equilibrium and represent regulation. Eventually, the system reequilibrates due to the balancing of gains and losses that control, or determine, the specific density at which equilibration occurs (which will probably not be the same equilibrium density that occurred prior to the perturbation). The initial increase can be used to estimate limitation (Equation (3)), and in this example (with natural rates of change equal to zero due to the equilibrium) is equal to the slope of the curve (i.e.,  $d[\log(\text{density})]/d(\text{time})$ ) immediately following the perturbation.

# Population Regulation and Density Dependence

## Detecting Density Dependence with statistical methods

1. **Key factor analysis** by life stages (Morris 1959; Varley and Gradwell 1960)

$$\log N(t+1) = \log N(t) + \log F + \log S_1 + \log S_2 + \dots$$

Where  $F$  = fecundity;  $S_i$  = survivorship from factor  $I$ ;

‘Killing power’  $k_i = -\log S_i$ ,

‘Total killing power’  $K = k_1 + k_2 + \dots + k_n$

Q: Which  $k_i$  is most correlated with  $K$ ?

# European spruce sawfly in New Brunswick, Canada

Analysis based on twice-per-year  
censuses from 1938-1962

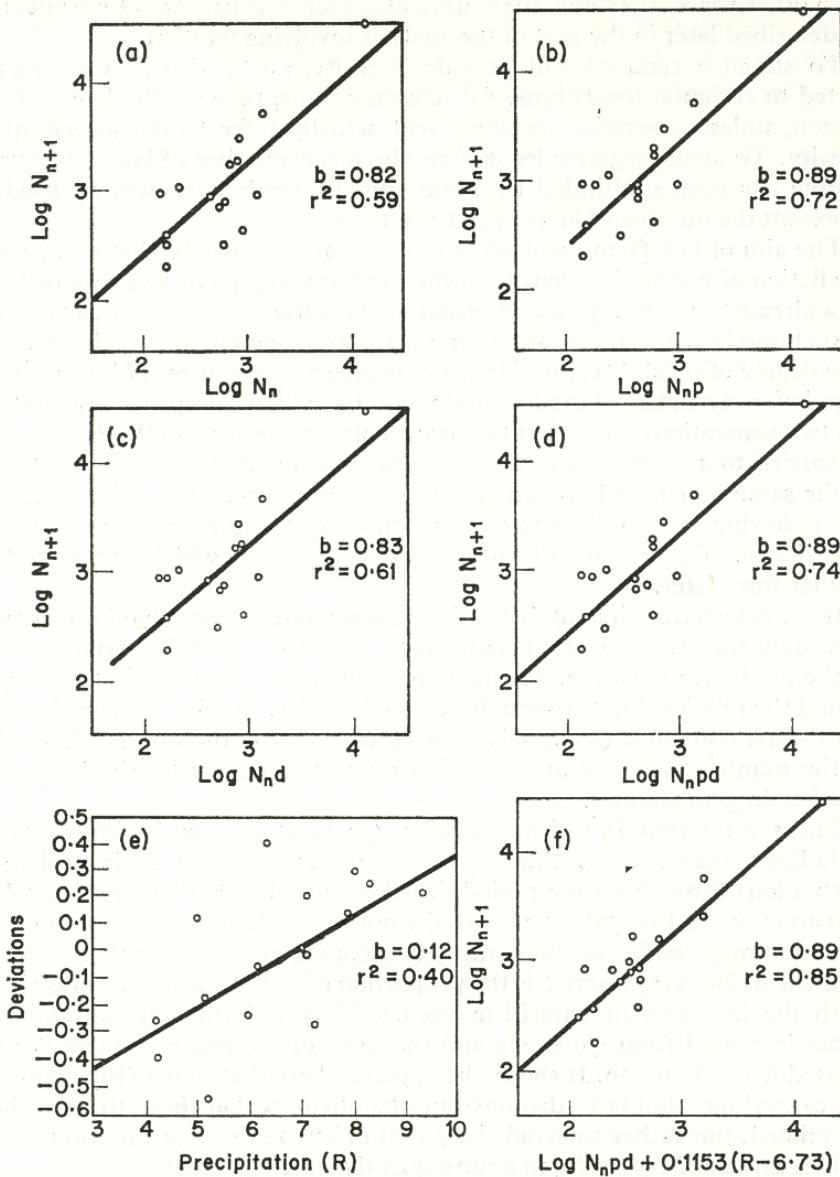


FIGURE 33. Scatter diagrams for the successive steps in the analysis of the European spruce sawfly data.  $N_n$  = number of larvae in generation 1 of any year;  $N_{n+1}$  = number of larvae in generation 2;  $p$  = proportion surviving parasitism;  $d$  = proportion surviving disease;  $R$  = May and June precipitation in inches (after Neilson and Morris 1964).

$N_n$  = # larvae in gen 1 of any year

$N_{n+1}$  = # larvae in gen 2 of same yr

$p$  = prop surviving parasitism

$d$  = prop surviving disease

$R$  = precipitation

From: Clark, L. R. 1967. The Ecology of Insect Populations in Theory and Practice. Methuen, London



# Key Factor Analysis

parasitism + disease

parasitism

TABLE II. Correlation and regression statistics for key-factor analysis for (a) generation 1 to generation 2 of the same year and (b) generation 2 of one year to generation 1 of the following year (after Neilson and Morris 1964).

		Correlation (r)	Per cent variance explained (100 r <sup>2</sup> )	Intercept* (F)	Slope (b)
(a) generation 1 to 2 same year	(1) log N <sub>n+1</sub> :log N <sub>n</sub>	0.77	59	0.75	0.82
	(2) log N <sub>n+1</sub> :log N <sub>n</sub> p	0.85	72	0.65	0.89
	(3) log N <sub>n+1</sub> :log N <sub>n</sub> d	0.78	61	0.72	0.83
	(4) log N <sub>n+1</sub> :log N <sub>n</sub> pd	0.86	74	0.65	0.89
	(5) Dev. from (4): May-June precip.	0.63	40	-0.78	0.12
	(6) log N <sub>n+1</sub> :log N <sub>n</sub> pd + 0.12(R-6.73)	0.92	58	0.65	0.89
Best predictive equation: log N <sub>n+1</sub> = log F + b <sub>1</sub> log N <sub>n</sub> pd + b <sub>2</sub> (R- $\bar{R}$ )					
		= 0.65 + 0.89 log N <sub>n</sub> pd + 0.12(R-6.73)			
(b) generation 2 to generation 1 following year	(1) log N <sub>n+1</sub> :log N <sub>n</sub>	0.60	36	1.10	0.57
	(2) log N <sub>n+1</sub> :log N <sub>n</sub> p	0.72	52	1.09	0.60
	(3) log N <sub>n+1</sub> :log N <sub>n</sub> d	0.65	42	1.04	0.60
	(4) log N <sub>n+1</sub> :log N <sub>n</sub> pd	0.77	60	1.04	0.64
Best predictive equation: log N <sub>n+1</sub> = log F + b <sub>1</sub> log N <sub>n</sub> pd					
		= 1.04 + 0.64 log N <sub>n</sub> pd			

\* Ordinate at log N<sub>n</sub>=0.

# Detecting Density Dependence

Problem 1: seldom have data detailed enough for this approach

Problem 2: density-dependence at one life stage is not adequate for regulation (Hassell 1986 TREE 1:90-93)

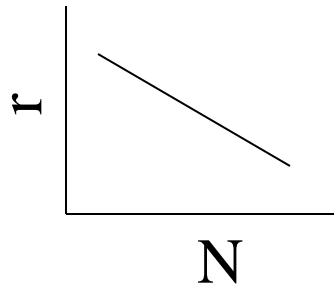
...Could be counter-acted by inverse density dependence in another stage

...Current analyses focus on inter-generational change in population size

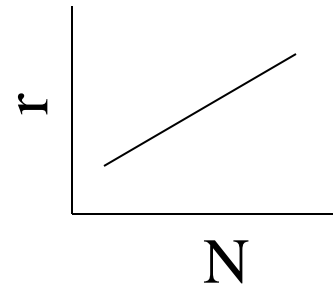
# Density-Dependence Tests

## 2. Analyses of Time Series

- Dependence of per capita growth rate on present and/or past population densities



Direct DD



Indirect DD

F.E. Smith (1961) published a criticism of Andrewartha and Birch: DD must be documented by analysis of  $r$ , not total population size, as in Davidson and Andrewartha (48)

# Detecting Density Dependence

## Analyses of Time Series

Problems:

- Low power (can't distinguish from random walk)
- Standard F-statistic is inappropriate
- Non-linearity and lags obscure relationships

However, new tests are available that overcome these problems.

# Detecting Density Dependence

Some consensus has been reached because:

1. Improved theory and statistical techniques
2. More and better data (longer time series)
3. More studies that combine observational data, field experiments, and mathematical theory

# Density-Dependence Tests

- Mixture of direct and inverse effects possible, summarized by ‘return tendency’
  - No DD of  $r$ , no return tendency, no stationary distribution of population densities
  - Also, DD is necessary but not sufficient condition for regulation... 3 conditions are:
    1. DD of correct sign (negative);
    2. DD strong enough to counteract disruptive effects of density independent factors;
    3. Lag for return must not be too long.
- \*See Nisbet and Gurney (1982); most analyses ignore strength and lag issues; most look for immediate DD in per capita growth rate

# Density-Dependence Tests

$$R_t = \ln N_t - \ln N_{t-1} = f(N_{t-1}) + \varepsilon_t$$

where  $f$  is typically a linear function of  $N_{t-1}$  or  $\ln N_{t-1}$  and  $\varepsilon_t$  is random density independent factors (Dennis and Taper 94)

*Criticisms:* linear, no delay, assumes errors are additive and independent. Properly used on semilparous univoltine organisms (must measure population size at one point each generation)... BUT this equation permits for a test of regulated dynamics

# Density dependence

## What data are needed and available?

Long time series heighten probability of detecting DD

Reviews:

- Woiwood & Hanski (92): 6000 pops of insects: aphids (94 spp) and moths (263 spp)
  - Sign DD in 69% aphids, 29% moths
  - Excluded time series less than 20 years and 84% of aphids and 54% of moths with DD
- Holyoak (93): 171 examples; also found that % with signif DD increases with length of time series
- Wolda and Dennis (93): Concluded freq of DD positively correlated with power to detect it
- Sibly et al. (05): Mammals, birds, fish, and insects may often overshooting K because of non-linear DD



# Density dependence

## What data are needed and available?

Note: DD and random walk may correspond for relatively large number of generations

10 years – prob of detecting DD different from random walk  
10%

30 years – Pr detection 60-70% (strength of DD and magnitude of exogenous variability)

Turchin (95) : regulation is ubiquitous, though any pop may not be regulated... especially if environment changes abruptly, as in human-caused changes

\* Role of DD test is to determine if stochastic equilibrium should be added to model of pop dynamics

# Density dependence

## What data are needed and available?

Turchin (95) continued:

Key questions:

- Are dynamics stationary?
  - Can add non-linear and time lag components to model (Poole 78. *Ann Rev Ecol&Syst* 9:427-448; Abrams. 2009. *Am Nat* 174:321-330)
- What are the relative role of endogenous and exogenous controls of dynamics?
- What is the degree of periodicity? (autocorrelation)
- What is degree of stability?
- Is regulation the result of local or regional (metapopulation) processes?
  - Old topic: Ehrlich and Birch. 1967. The “balance of nature” and “population control.” *Am Nat.* 101:97-107
  - Spreading risk, Andrewartha and Birch. 1984. *The Ecological Web.* Univ Chicago Press.
  - Huffaker and Kennett. 1956. deserves special mention, though usually discussed in pred-prey context