Lecture 2. Density-dependent population growth models: logistic, Ricker, and Schaefer models; maximum sustained yield.

Reading:

Gotelli, 2001, A Primer of Ecology, Chapter 2, pages 25-48.

Derivation of logistic equation: First, review notation for density-independent growth.

$N_{t+1} = N_t + N_t \times R = N_t \times (1 + R)$, $N_t = N_0 (1 + R)^t$

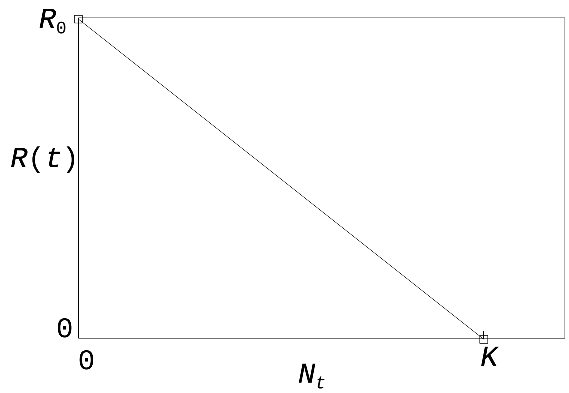
$N_{t+1}/N_t = 1 + R = \lambda$ = annual rate of increase

Finite rate of growth (R)

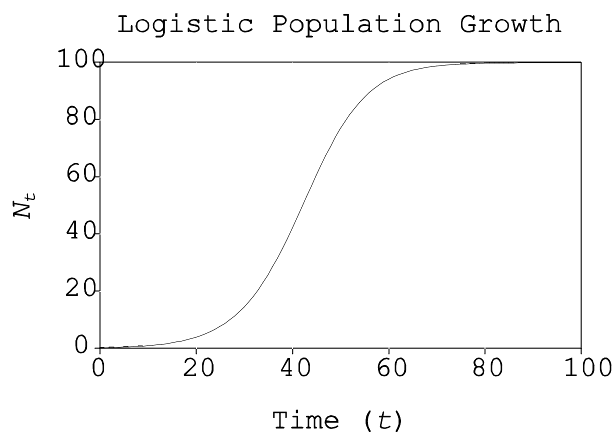
R = finite birth rate - finite death rate + finite immigration rate - finite emigration rate

Now, let R be a function of population size, N_t [and hence time, $R(t)$], such that

$$R(N_t) = R(t) = R_0\left(1 - \frac{N_t}{K}\right)$$



With this function $R(t) = f(N_t, K)$, the following population growth curve results:



K is carrying capacity, threshold at which population growth is zero, negative above.

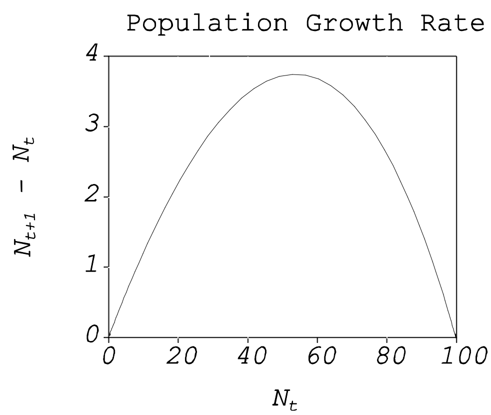
$$N_{t+1} = N_t\left[1 + R_0\left(1 - \frac{N_t}{K}\right)\right]$$

Per capita finite rate of increase

$$\frac{N_{t+1} - N_t}{N_t} = R_0 - \frac{R_0 N_t}{K}$$

Concept of Maximum Sustained Yield (MSY)

To see graphically the population size that provides the maximum sustainable harvest from a population, plot the population size against the annual increment:



To analytically examine MSY, recognize that we want to maximize the annual increase in the population, i.e., $N_{t+1} - N_t = N_t R_0(1 - N_t/K) = R_0 N_t - (R_0/K)N_t^2$. To maximize this equation with respect to N_t, we can take the derivative and set the result to zero. Thus,

$$\frac{\partial(N_{t+1} - N_t)}{\partial N_t} = R_0 - \frac{2R_0 N_t}{K} \quad .$$

Setting this result equal to zero and solving for N_t gives the value of N_t that maximizes the annual increase in the population:

$$R_0 - \frac{2R_0 N_t}{K} = 0 \quad ,$$

giving the result that $N_t = K/2$. Now, we can plug this value back into the equation for the annual increase to solve for the amount of annual harvest:

$$N_{t+1} - N_t = R_0 N_t\left(1 - \frac{N_t}{K}\right) = R_0\frac{K}{2}\left(1 - \frac{K/2}{K}\right) = \frac{R_0 K}{4} \quad .$$

Thus, if the population size is $K/2$, then $R_0K/4$ animals can be harvested each year. However, consider the assumptions being made to obtain this result: a deterministic population growth process with no age or sex structure, just for starters. Even though the result has a lot of theoretical importance, its practical importance for management is negligible.

Because the solution to the differential equation is seldom presented, I have done so here. Start with the differential equation.

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

Separating variables gives

$$\frac{dN}{N(K - N)} = \frac{r}{K}dt$$

Now integrating each side

$$\int \frac{dN}{N(K - N)} = \int \frac{r}{K}dt$$

Performing the 2 integrations and adding a constant of integration *c* gives

$$\frac{\ln(N)}{K} - \frac{\ln(N - K)}{K} = \frac{rt}{K} + c$$

Solving for *c* at $t = 0$ and $N = N_0$ gives

$$c = \frac{\ln(N_0)}{K} - \frac{\ln(N_0 - K)}{K}$$

Substituting this expression for c gives

$$\frac{\ln(N)}{K} - \frac{\ln(N - K)}{K} = \frac{rt}{K} + \frac{\ln(N_0)}{K} - \frac{\ln(N_0 - K)}{K}$$

Taking the exponential of both sides gives

$$\frac{N}{N - K} = \frac{N_0 e^{rt}}{N_0 - K}$$

Now solving for N gives

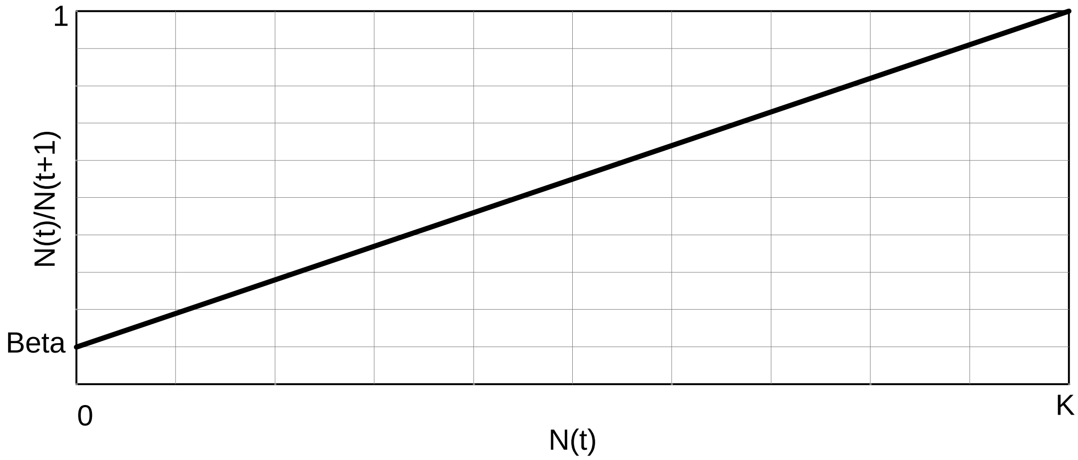
$$N = \frac{K}{1 + \left(\frac{K}{N_0} - 1\right) e^{-rt}}$$

Derivation of Ricker's equation. W. E. Ricker (1954) invented this equation to model fishery stocks (also see Ricker 1975:282). It is a discrete population model:

$$N_{t+1} = N_t \exp\left[R_0\left(1 - \frac{N_t}{K}\right)\right] .$$

Note that the density dependence in this model becomes stronger at higher densities, due to the exponential function.

Density-dependent population growth is more than the logistic curve, with many possibilities existing. Ricker's model is just one example. Getz (1996) suggests that the strongest effect of density should occur as population growth rate approaches zero, i.e., the population approaches carrying capacity. Note that for the logistic function, the effect of density is constant because the relationship is linear. Getz (1996), Burgman et al. (1993) and May and Oster (1976) summarize other functional relationships to incorporate density dependence. For example, assume a linear relationship between N_t/N_{t+1} and N_t:



From this line, the equation

$$\frac{N_t}{N_{t+1}} = \beta + \frac{1 - \beta}{K} N_t$$

is derived, with intercept β and slope $\frac{1 - \beta}{K}$. The resulting population growth model is

$$N_{t+1} = \frac{KN_t}{K\beta + (1 - \beta)N_t} \quad .$$

By taking the limit of the per capita rate of population growth as N_t approaches zero, we find that R_0 can be specified as a function of the parameter β as

$$R_0 = \frac{1 - \beta}{\beta} \quad ,$$

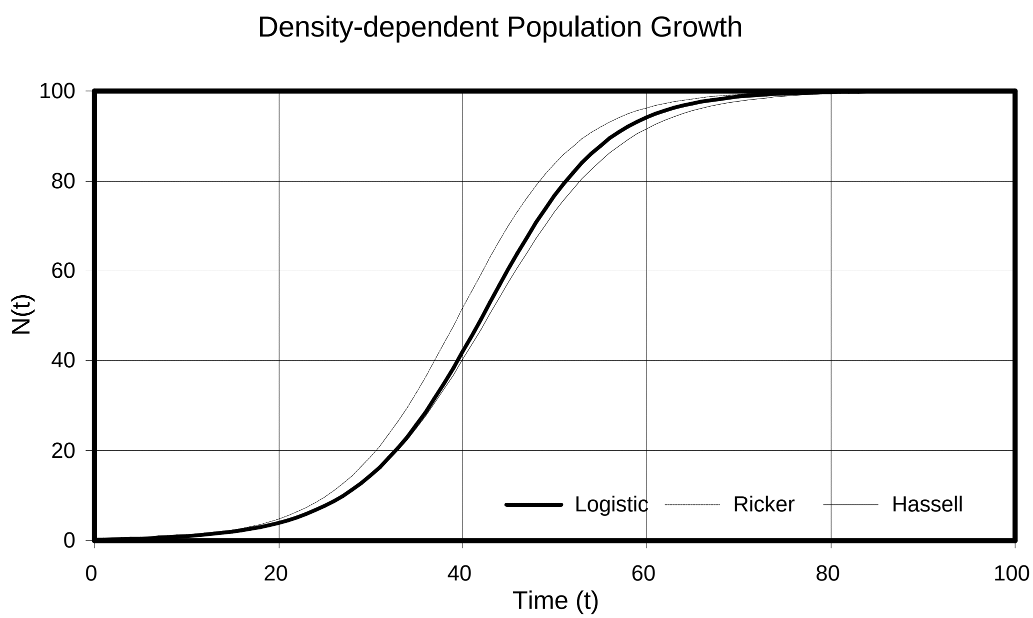
giving the following parameterization of the model:

$$N_{t+1} = \frac{KN_t(R_0 + 1)}{K + N_t R_0} \quad .$$

This model is generalized by Hassell (1975), Hassell et al. (1976) and May (1976) as

$$N_{t+1} = \frac{\lambda N_t}{(1 + aN_t)^b} \quad .$$

The following graph demonstrates the similarity of the 3 models for R_0 = 0.15 and K = 100.



The following table provides a comparison of the models in terms of the per capita growth rate and λ.

Model	Model Equation	$R(t)$	λ
logistic	$N_{t+1} = N_t\left[1 + R_0\left(1 - \frac{N_t}{K}\right)\right]$	$R_0\left(1 - \frac{N_t}{K}\right)$	$+ R_0\left(1 - \frac{N_t}{K}\right)$
Ricker	$N_{t+1} = N_t \exp\left[R_0\left(1 - \frac{N_t}{K}\right)\right]$	$\exp\left[R_0\left(1 - \frac{N_t}{K}\right)\right] - 1$	$\text{xp}\left[R_0\left(1 - \frac{N_t}{K}\right)\right]$
Hassell	$N_{t+1} = \frac{KN_t(R_0 + 1)}{K + N_tR_0}$	$\frac{1 + R_0}{1 + R_0\frac{N_t}{K}} - 1$	$\frac{1 + R_0}{1 + R_0\frac{N_t}{K}}$

Two other examples of models of density dependence include Beverton and Holt (1957) and Ricker (1975:291)

$$N_{t+1} = \frac{1}{\rho + (k/N_t)} \quad ,$$

and Maynard-Smith and Slatkin (1973)

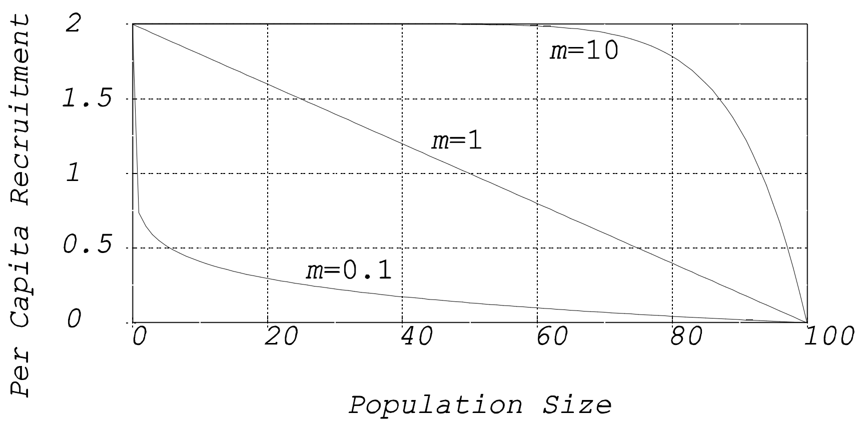
$$N_{t+1} = \frac{rN_t}{1 + (\rho N_t)^q} \quad .$$

Each of these models of density dependence results in a different relationship between per capita recruitment and population size. As a result, the density dependence is implemented differently at a particular population levels, and population viability is somewhat affected. Distinguishing between these various models with data is generally not practical because the stochasticity of observed population growth covers up the small distinctions between the models.

Richards model. Rather than modeling per capita rates of change as linear functions, more complex, nonlinear, functions can be substituted, as shown above. An example is the Richard's curve (Fowler 1981), where the per capita recruitment is

$$R_t = R_0\left[1 - \left(\frac{N_t}{K}\right)^m\right]$$

with the exponent *m* changing the shape of the relationship from linear to either concave or convex. For $m = 10$, density dependence is not invoked until the population approaches K. For $m = 1$, density dependence is invoked at a constant rate as the population grows. For $m = 0.1$, density dependence is invoked most strongly at low densities, and relaxes as the population grows. MSY shifts from low on the curve ($m < K/2$) to close to K ($m > K/2$).



Fowler (1981) argues that both theory and empirical information support the conclusion that most density-dependent change occurs at high population levels (close to the carrying capacity) for species with life history strategies typical of large mammals, such as deer ($m > 1$). The reverse is true for species with life history strategies typical of insects and some fishes, with $m < 1$). McCullough (1990) also elaborates on this concept, and suggests that the spatial scale of the population being measured and environmental heterogeneity affect the degree to which deer populations demonstrate density dependence near K carrying capacity.

Sæther et al. (2002) used the theta-logistic model (equivalent to the Richards model described here) to show that in long-lived species like the south polar skua, density dependence has the greatest influence on the dynamics of the populaiton when the size of the population is close to carrying capacity. In contrast, in shorter-lived birds, the effect of density dependence is greater at lower relative densities.

Schaefer model (see Bulmer 1994:116-120) -- In this section, a traditional derivation of the maximum sustainable yield (MSY) concept is provided. I'll use a differential equation to develop MSY because the mathematics are easier to do, and because this is the traditional approach. The approach and results are applicable to the difference equation also. Modify the logistic differential equation to include exploitation:

$$\frac{dN}{dt} = f(N) = R_0\left(1 - \frac{N}{K}\right)N - h(N)$$

where *h(N)* is the rate of harvest or fishing. Under the catch per unit effort model (catch is a linear function of effort), assume that $h(N) = qEN$, where *E* is the fishing effort (e.g., number of vessel days per unit time) and *q* is a constant called the "catchability" coefficient. Absorb *q* into *E*, so that

$$\frac{dN}{dt} = f(N) = R_0\left(1 - \frac{N}{K}\right)N - EN$$

If *E* is constant and $<R_0$, then a unique nonzero equilibrium exists at the point $\hat{N} = K(1 - E/R_0)$, i.e., $dN/dt = 0$. The equilibrium harvest or sustained yield at this point is

$$\hat{H} = E\hat{N} = KE\left(1 - \frac{E}{R_0}\right)$$

The sustained yield is maximized when $E = R_0/2$, giving an equilibrium population size of $\hat{N} = K/2$ and a maximum sustainable yield (MSY) of $R_0K/4$.

Impact of stochasticity on harvest. Aanes et al. (2002) discuss 5 different harvesting strategies, none of them based on the MSY concept. When stochasticity is recognized in the population, both in the form of annual variation in true population size, and variation due to estimates of population size instead of truth, alternative harvest strategies will provide a more effective harvest strategy. More on this topic will be included in the management lecture.

Ecological considerations in fisheries managment. Link (2002) discusses the importance of including ecological processes (predation, competition, environmental regime shifts, and habitat alteration) in fisheries management. Basically, he is arguing that the simplistic models presented here are inappropriate to manage a fishery, particularly when the population is has low stock abundance.

Literature Cited

Aanes, S., S. Engen, B.-E. Sæther, T. Willebrand, and V. Marcstrom. 2002. Sustainable harvesting strategies of willow ptarmigan in a fluctuating environment. Ecological Applications 12:281-290.

Bulmer, M. 1994. Theoretical evolutionary ecology. Sinauer Associates, Inc., Sunderland, Massachusetts, USA. 352 pp.

Burgman, M. A., S. Ferson, and H. R. Akçakaya. 1993. Risk assessment in conservation biology. Chapman and Hall, London, United Kingdom. 314 pp.

Fowler, C. W. 1981. Density dependence as related to life history strategy. Ecology 62:602-610.

Getz, W. M. 1996. A hypothesis regarding the abruptness of density dependence and the growth rate of populations. Ecology 77:2014-2026.

Hassel, M. P. 1975. Density-dependence in single-species populations. Journal of Animal Ecology 44:283-295.

Hassell, M. P., J. H. Lawton, and R. M. May. 1976. Patterns of dynamical behaviour in single-species populations. Journal of Animal Ecology 45:471-486.

Link, J. S. 2002. Ecological considerations in fisheries management: when does it matter? Fisheries 27(April):10-17.

May, R. M. 1976. Models for single populations. Pages 4-25 *In* Ecology: Principles and Applications. R. M. May, ed. Blackwell, Oxford, United Kingdom.

May, R. M., and G. F. Oster. 1976. Bifurcations and dynamic complexity in simple ecological models. American Naturalist 110:573-600.

Maynard-Smith, J. and M. Slatkin. 1973. The stability of predator-prey systems. Ecology 54:384-91.

McCullough, D. R. 1990. Detecting density dependence: filtering the baby from the bathwater. Transactions of the North American Wildlife and Natural Resources Conference 55:534-543.

Ricker, W. E. 1954. Stock and recruitment. Journal Fisheries Research Board of Canada

11:624-651.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada, Bulletin 191. Ottawa, Canada.

Sæther, B.-E., S. Engen, and E. Matthysen. 2002. Demographic characteristics and population dynamical patterns of solitary birds. Science 295:2070-2073.