Short Communication

Dynamics of populations with nonoverlapping generations, continuous mortality, and discrete reproductive periods

A.L. Jensen

School of Natural Resources, University of Michigan, Ann Arbor, MI 48109-1115, USA

Abstract

Simple nonlinear difference equations have been used to describe the growth of populations with nonoverlapping generations; these equations assume mortality and recruitment to be discrete and instantaneous. In reality, mortality is more or less continuous and recruitment is more or less continuous over discrete intervals of time. This information was incorporated into the discrete time form of the logistic equation and the closed form solution was obtained. The population growth rate depends on recruitment, mortality, duration of the lifespan, and timing of the reproductive period. Population stability depends on the population growth rate, and therefore, stability also depends on the above factors. A stable population occurs with high mortality and a relatively short reproductive period. Under certain conditions a relatively small decrease in mortality can cause the dynamical behavior of a population to change drastically.

Key words: Population dynamics

1. Introduction

May (1974, 1986) suggests that an appropriate mathematical description for populations with nonoverlapping generations is nonlinear difference equations. The simplest such model is the discrete time form of the logistic equation (May, 1974). At least two discrete time forms of the logistic equation have been widely used (May, 1974); here I will use the form

$$N_{t+1} = N_t(1+r) - rN_t^2/K,\tag{1}$$

where N is population abundance, r is the population growth rate, and K is the carrying capacity or mean equilibrium population abundance.

The mathematical behavior of the discrete time model is complex compared to that of the continuous time model; May (1974) shows that Eq. 1 has stable

equilibrium points for $0 < r < 2$, stable cycles of period 2^n for $2 < r < 2.572$, and chaotic behavior, where cycles depend on the initial condition, with $r > 2.572$. The continuous time logistic equation has a globally stable equilibrium at $N = K$ for all $r > 0$ (May, 1974). The complex behavior of the discrete time model could explain some of the fluctuations observed in biological populations.

Ricker (1954) developed and applied a model similar to Eq. 1 to relate spawners in a fish stock to recruits, but in his model there was no mortality between recruitment periods. To describe baleen whale populations May (1980) used a first-order difference-delay equation in which a discrete time mortality equation was combined with a discrete time form of the logistic equation applied as a recruitment function.

Neither the discrete time model nor the continuous time model gives a good description of most population growth. The discrete time model assumes that both mortality and recruitment occur instantaneously. For most populations there is a reproductive period that is more or less discrete, but it usually spans a considerable part of the lifespan, and reproduction is more or less continuous during the reproductive period. Mortality occurs throughout the lifespan, and thus it is more or less continuous even in populations where individuals die after reproduction. I have investigated the dynamics of a simple population model that assumes continuous mortality and reproduction that occurs continuously over an interval of time.

2. Model development

Rather than apply the logistic equation for abundance as May (1974) did, the logistic model was used for recruitment during a reproductive period and mortality was assumed continuous during the lifespan. Let:

$R_t(x)$ = number of recruits of age x in time period or generation t,

$S_t(x)$ = number of spawners of age x in time period t,

   t = time period or generation number; a discrete time variable,

   x = age or time within a generation; a continuous variable within a generation.

Both S and R are always functions of t and x, but for notational simplicity they sometimes will be written as S_t and R_t. The recruits of time period t were born during time period t and are not mature. The spawners during time period t were born during time period $t - 1$ and will mature during time period t.

During a generation, change in number of recruits is given by the components balance equation

$$\mathrm{d}R_t/\mathrm{d}x = (\mathrm{d}R_t/\mathrm{d}x)_{\mathrm{birth}} - (\mathrm{d}R_t/\mathrm{d}x)_{\mathrm{death}}, \tag{2}$$

and the rate of birth is described by the equation

$$(\mathrm{d}R_t/\mathrm{d}x)_{\mathrm{birth}} = 0, \qquad\qquad x < p \tag{3}$$

$$(\mathrm{d}R_t/\mathrm{d}x)_{\mathrm{birth}} = aS_t - aS_t^2/R_m, \quad x \geqslant p \tag{4}$$

where p is age at maturity, R_m is the maximum number of recruits, a is the population recruitment rate, and S_t is the number of spawners of age x at time t.

The mortality of recruits is

$$(dR_t/dx)_{death} = -ZR_t, \quad x \geqslant p, \tag{5}$$

where Z is a mortality coefficient. The mortality of spawners is

$$dS_t/dx = -ZS_t, \quad 0 \leqslant x \leqslant g, \tag{6}$$

where g is the duration of a generation. For simplicity it is assumed that spawners and recruits have the same mortality. Bringing these equations together gives

$$dR_t/dx = aS_t - aS_t^2/R_m - ZR_t, \quad x \geqslant p. \tag{7}$$

At the end of generation t, the number of spawners of generation $t + 1$ is obtained from the number of recruits of generation t as

$$S_{t+1}(x) = R_t(g)e^{-Zx}, \tag{8}$$

and this equation connects generations. Solution of Eq. 7 gives the number of recruits of age x during generation t as

$$R_t(x) = aR_{t-1}(ge^{-Zx} - pe^{-Zp}) + aR_{t-1}^2(e^{-2Zx} - e^{-2Zp})/ZR_m \tag{9}$$

and at the end of the lifespan of generation t

$$R_t(g) = aR_{t-1}(ge^{-Zg} - pe^{-Zp}) + aR_{t-1}^2(e^{-2Zg} - e^{-2Zp})/ZR_m, \tag{10}$$

where g is the duration of the lifespan, p is the age when the reproductive period begins, and R_{t-1} is $R_{t-1}(g)$.

3. Results and discussion

Eq. 10 can be written in the same general form as the discrete time logistic equation (Eq. 1), but in terms of recruits rather than population abundance, and with

$$r = a(ge^{-Zg} - pe^{-Zp}) - 1, \tag{11}$$

$$K = \frac{ZR_m(ge^{-Zg} - pe^{-Zp})}{e^{-2Zg} - e^{-2Zp}}. \tag{12}$$

Eq. 12 indicates that the carrying capacity is determined by the mortality rate, maximum reproductive rate, lifespan, and age at maturity. Eq. 11 indicates that high population growth rates are associated with longer reproductive periods, lower mortality rates, and higher recruitment rates. The population growth coefficient decreases exponentially with increase in Z, and the rate of decrease depends on the recruitment rate and duration of the reproductive period.

For Eq. 10 to be biologically meaningful it is necessary that

$$(e^{-2Zg} - e^{-2Zp}) < 0 \quad \text{and} \tag{13}$$

$$(ge^{-Zg} - pe^{-Zp}) > 0. \tag{14}$$

Table 1
Dynamics of a population described by Eq. 1 (May, 1974)

Dynamical behavior	Value of population behavior growth rate
Stable equilibrium point	$2 > r > 0$
Stable cycles of period 2^n	
2	$2.449 > r > 2.000$
4	$2.544 > r > 2.449$
8	$2.564 > r > 2.544$
16, 32, 64,...	$2.570 > r > 2.564$
Chaotic	$r > 2.570$

The first of these inequalities requires $g > p$, and the second places an upper bound on the instantaneous mortality rate. The second inequality gives

$$Z < \frac{\log \, g - \log \, p}{g - p} \, ; \qquad (15)$$

that is, the mortality that a population can survive depends on the age at maturity and duration of the reproductive period. If mortality is high and maturity does not occur quickly enough, or if the reproductive period is not long enough, the population growth rate will be less than zero and the population will become extinct.

May (1974) investigated stability properties of the discrete time form of the logistic equation, and he found the values of r for which Eq. 1 has a stable equilibrium, cycles, and chaotic behavior (Table 1). May's (1974) results can be applied to Eq. 10 to investigate these same relations for populations with continuous mortality and discrete reproduction. Dynamics of a population with a 365-day lifespan and maturity at day 335 were determined for different values of the recruitment rate (a) and different values of the daily instantaneous mortality coefficient (Z). The values of the mortality rate that result in extinction, stability, cycles, and chaotic behavior were calculated for different values of the recruitment rate by setting r at the appropriate value (Table 1) and then solving for Z numerically in Eq. 10. If the recruitment rate is low, there are neither cycles nor chaotic behavior for any mortality rate (Table 2). For larger values of the recruitment rate, the population moves from stability through cycles to chaotic behavior as the mortality rate decreases (Table 2). In general, the decrease in mortality necessary to move from stability to cycles and chaotic behavior is not large, and as the recruitment rate increases the decrease in mortality necessary to change population behavior decreases.

For populations with nonoverlapping generations there is a range of possible dynamical behaviors. If survival is low, population abundance is stable, but if survival increases because, for example, of favorable environmental conditions, the population could become unstable and exhibit large fluctuations in abundance. Through effects on mortality, environmental factors can change the pattern of population growth.

Table 2
Dynamics of a population with a 365-day lifespan and reproductive period beginning at day 335 for different values of the recruitment rate (a) as a function of the daily instantaneous mortality coefficient (Z)

a	Dynamics of population	Z
0.10	Extinction	$Z > 0.00134$
	Stable	$0.001337 > Z > 0$
	Cycles	none
	Chaotic	none
0.25	Extinction	$Z > 0.00207$
	Stable	$0.00207 > Z > 0.00115$
	Cycles	$0.00115 > Z > 0.00096$
	Chaotic	$Z < 0.00096$
0.50	Extinction	$Z > 0.00242$
	Stable	$0.00242 > Z > 0.00179$
	Cycles	$0.00179 > Z > 0.00165$
	Chaotic	$Z < 0.00165$
0.75	Extinction	$Z > 0.00255$
	Stable	$0.00255 > Z > 0.00207$
	Cycles	$0.00207 > Z > 0.00196$
	Chaotic	$Z < 0.00196$

Cycles do not occur with survival between generations because if large numbers survive there is a large overlap of generations, and cycles then do not occur because growth follows the continuous time model, but if few survive, so population growth resembles population growth with no overlap, mortality is high and even in populations with no overlap there are no cycles under this condition.

Acknowledgments

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