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"Exploitation of One Population in Peaceful, Stochastic & Periodic Environment"

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HARVESTING POPULATION IN A PERIODIC ENVIRONMENT

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ABSTRACT

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Maximum sustainable average yield rate (MSAY) of a logistic population using constant effort harvesting strategy in an environment where intrinsic growth rate is a random variable in the form of white noise, is well known. When the variance of environmental fluctuations increases the optimum effort decreases linearly while MSAY decreases quadratically.

In an environment where carrying capacity varies periodically and the intrinsic growth rate is constant, the optimum harvesting effort is not affected by a change in the frequency of environmental variation, but, an increase in the frequency will decrease MSAY rate.

INTRODUCTION

Models are often investigated as a basis for choosing a suitable strategy for exploitation of natural populations. Attributes of a suitable harvesting strategy include automatic protection against extinction and achievement of the maximum sustainable average yield rate (MSAY). MSAY and corresponding optimum effort have been found in the case of a population living in a constant (for example Clark, 1976) and randomly fluctuating environment (Gatto and Rinaldi, 1976; Beddington and May, 1977).

In this paper the authors consider the problem of harvesting one population in a periodically varying environment. Only the constant effort harvesting strategy is investigated since it has been found to be superior to the constant quota, due to its stabilizing property.

HARVESTING POPULATIONS IN CONSTANT AND STOCHASTIC ENVIRONMENT

Let the population growth follow logistic law. The equations which govern population dynamics under constant quota and constant effort harvesting

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are respectively:
(a) constant quota

$$\frac{dN}{dt} = rN(1 - N/K) - q \tag{1}$$

(b) constant effort harvesting

$$\frac{dN}{dt} = rN(1 - N/K) - eN \tag{2}$$

where, r is the intrinsic growth coefficient, K carrying capacity of the environment, and q and eN are yield rates.

It is well known that for both strategies maximum sustainable yield rate is $rK/4$. In the case of constant effort strategy, MSY is obtained by applying optimum effort intensity $e_{opt} = r/2$ which results in $N^* = K/2$. Constant effort strategy leads to a stable population equilibrium while constant quota leads to an unstable equilibrium. Hence, constant effort strategy should be favoured and is considered below.

In a randomly fluctuating environment with $r(t) = r_0 + \gamma(t)$ where r_0 is the mean value and $\gamma(t)$ is white noise with the mean equal to zero and variance σ^2, average yield $\langle Y \rangle_R$ and the coefficient of variation CV_y of the yield are respectively (Beddington and May, 1977):

$$\langle Y \rangle_R = Ke(r_0 - e - \sigma^2/2)/r_0 \tag{3}$$

and

$$CV_y = \left(\frac{\sigma^2/2}{r_0 - e - \sigma^2/2} \right)^{1/2} \tag{4}$$

Taking $\partial\langle Y \rangle_R/\partial e = 0$ we find that the optimum harvesting effort is:

$$e_{opt} = \frac{r_0}{2}(1 - \sigma^2/2r_0) \tag{5}$$

It should be noted that the optimum harvesting effort is smaller in a randomly fluctuating environment than in the constant environment. In addition, if the population is found to be embedded in an environment characterized by such random environmental fluctuations that $\sigma^2 = 2r_0$ then harvesting of such a population should be forbidden. For another example of environmental characteristics which should cause harvesting to be forbidden see Gatto and Rinaldi, 1976. Hence, the population in such an environment cannot be called a harvesting resource.

Substituting eq. 5 into eqs. 3 and 4:

$$MSAY_R = \frac{r_0 K}{4}(1 - \sigma^2/2r_0)^2 \tag{6}$$

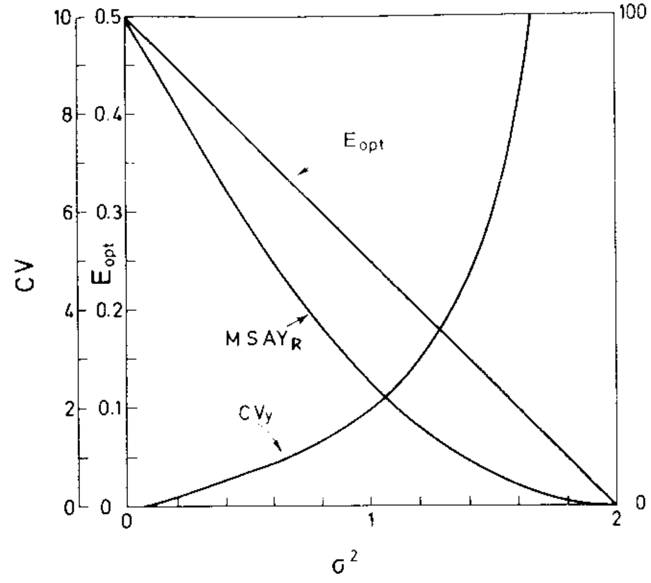

Fig. 1. Optimum effort intensity (e_{opt}), maximum sustainable average yield ($MSAY_R$) and coefficient of variation of the yield (CV) as a function of σ^2 ($r = 1$, $K = 400$).

The corresponding coefficient of variation is:

$$CV_{MSAY} = \frac{\sigma}{\sqrt{r_0 - \sigma^2/2}} \tag{7}$$

Thus, $MSAY_R$ is smaller than MSY in a constant environment. As the variance of random fluctuations increases, e_{opt} decreases linearly while $MSAY_R$ decreases quadratically (see Fig. 1).

POPULATION IN A PERIODIC ENVIRONMENT

The environment in which most populations live varies periodically. This means that model parameters which represent the environment should be periodic functions of time.

For any $r = r(t)$ and $K = K(t)$ with the substitution $x = 1/N$, the logistic equation can be converted into linear form. Solving the equation gives:

$$\frac{1}{N} = \frac{1}{N_0}\exp\left(-\int_0^t r(t')\,dt'\right) + \int_0^t \frac{r(t')}{K(t')}\exp\left(-\int_{t'}^t r(t'')\,dt''\right)dt' \tag{8}$$

When r is a constant, Eq. 8 becomes:

$$\frac{1}{N} = \frac{1}{N_0}\exp(-rt) + r\int_0^t \frac{\exp(-r(t-t'))}{K(t')}\,dt' \qquad (9)$$

The asymptotic solution is the second term on the right side of Eq. 9.

Let $K(t) = K_0 + K_1 \cos \omega t$, with $K_0 > K_1$. Two interesting cases can be distinguished (May, 1978).

Case 1: $r \ll \omega$

The asymptotic solution becomes:

$$N(t) \rightarrow \left(\frac{\omega}{2\pi}\int_0^t \frac{dt'}{K(t')}\right)^{-1}\left(1 + 0\left(\frac{2\pi r}{\omega}\right)\right) \qquad (10)$$

Neglecting the term of the order $2\pi r/\omega$ one obtains:

$$N \rightarrow \sqrt{K_0^2 - K_1^2} \qquad (11)$$

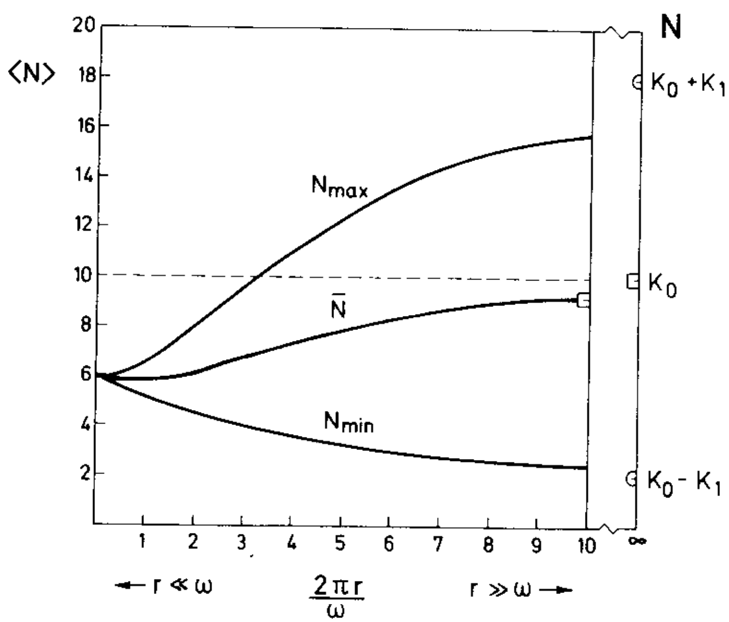

Fig. 2. Amplitude of variation in population numbers, N, as a function of $2\pi r/\omega$. The upper curve denotes the maximum (N_{max}) and the lower curve denotes the minimum (N_{min}) values of population numbers for large times. The middle curve denotes the mean ($\bar{N}$). As $2\pi r/\omega \rightarrow 0$, $N_{max} \rightarrow K_0 + K_1$, $\bar{N} \rightarrow K_0$ and $N_{min} \rightarrow K_0 - K_1$ ($r = 1$, $K_0 = 10$, $K_1 = 8$).

Case 2: $r \gg \omega$

The asymptotic solution becomes:

$$N(t) \rightarrow (K_0 + K_1 \cos \omega t)\left(1 + 0\left(\frac{\omega}{2\pi r}\right)\right) \qquad (12)$$

According to May these results were first obtained by Poluektov (1974) and by Kiester and Barakat (1974).

What remains to be investigated is the dynamic behaviour of a logistic population between the two extreme cases. One can do this by a set of numeric experiments. Figure 2 shows some properties of asymptotic behaviour for varying frequencies. As expected, the variation in population numbers increases as the ratio r/ω increases. This ratio measures the ability of the population to track environmental variation.

In general it has been proven that the asymptotic solution is periodic and globally stable (Butler and Freeman, 1981). To prove that the asymptotic solution has a period $2\pi/\omega$, periodicity is assumed and the second term on the right side of Eq. 9 is differentiated.

Results similar to eqs. 11 and 12 can be obtained for a larger class of periodic functions (see Appendix).

CONSTANT EFFORT HARVESTING IN A PERIODIC ENVIRONMENT

Assume that the logistic population is harvested according to a constant effort strategy in an environment characterized by $K(t) = K_0 + K_1 \cos \omega t$. The population dynamics will be governed by:

$$\frac{1}{N(t)} = \frac{1}{N_0}\exp(-(r-e)t) + r\int_0^t \frac{\exp(-(r-e)(t-t'))}{K(t')}\,dt' \qquad (13)$$

Since the first term on the right side decreases to zero as t increases, the asymptotic behaviour is determined by the second term. Because the authors did not succeed in solving the integral analytically, the two extreme cases are reconsidered.

Case 1: $r - e \ll \omega$

The net intrinsic growth coefficient is much smaller than the frequency of environmental variation. This means the variations are levelled out by the population. The asymptotic value of the population number is:

$$N_1 = \sqrt{K_0^2 - K_1^2}\,(1 - e/r) \qquad (14)$$

Since the yield rate is eN_1, the optimum effort obtained by maximizing the yield is $e_{opt} = r/2$, the same as in constant environment. The asymptotic value of MSY is:

$$MSY_1 = \left(r\sqrt{K_0^2 - K_1^2}\right)/4 \quad (15)$$

MSY_1 becomes significantly smaller than in the constant environment ($K = K_0$) when $K_0/2 < K_1 < K_0$.

Case 2: $r - e \gg \omega$

In this case the population easily tracks environmental variations. For large times the population $N(t)$ tends to $N_2(t)$:

$$N_2(t) = (K_0 + K_1 \cos \omega t)(1 - e/r) \quad (16)$$

The mean yield rate averaged over one cycle is approximately:

$$Y_2 = K_0 e(1 - e/r) \quad (17)$$

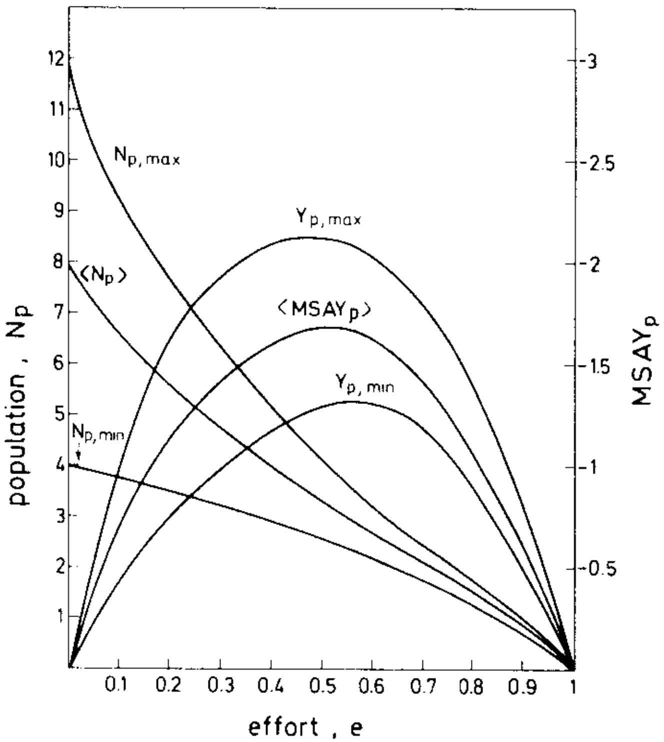

Fig. 3. Variations in N and $MSAY_p$ for various effort intensities. The upper curve denotes maximum (N_{max} and Y_{max}) and the lower curves denote minimum (N_{min} and Y_{min}) values of population numbers and yield rates, respectively. The middle curve denotes means (N and MSAY) over one period. ($r = 1$, $\omega = \pi/2$, $K_0 = 10$, $K_1 = 8$).

The effort which corresponds to the MSAY rate is again $r/2$. It follows from Eq. 17 that the $MSAY_2$ rate is the same as MSY in the constant environment.

Changes in population variation and in yield can be investigated numerically for various effort levels (Fig. 3). A harvested population has smaller average numbers and smaller variations. As the effort approaches e_{opt} variations in the yield increase. As in the constant environment an attempt to increase the effort beyond e_{opt} results in a decreased yield.

Characteristic return time in both cases is identical to the one in the constant environment: $T = 1/(r - e)$.

CONCLUSION

Constant effort (proportional) harvesting of logistic populations in an environment where carrying capacity varies periodically decreases population variations. Optimum harvesting effort which gives maximum sustainable (average) yield is $r/2$, which is the same as when harvesting logistic populations in a constant environment. The resulting MSAY is equal to (for $r \gg \omega$) or smaller than MSY in a constant environment.

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APPENDIX

Assume that $1/K(t) = f(t)$, where $f(t)$ is an absolutely continuous periodic function. Recall the following definition and the theorem.

Definition f: $a, b \to R$ is absolutely continuous if $\forall \epsilon > 0$, $\delta > 0$. For every finite family of disjoint intervals (a_k, b_k), $k = 1, \ldots, m$ of measure smaller than δ; i.e. for $\sum_1^m (b_k - a_k) < \delta$ the following condition holds:

$$\sum_1^m |f(b_k) - f(a_k)| < \epsilon$$

Theorem: Let f: $R \to R$ an absolutely continuous function with period T and $f' \in L_2[-T/2, T/2]$, then the Fourier series of f converges uniformly by points to f on R.

Choose T so that it satisfies the conditions of the theorem. It is then possible to integrate the Fourier series term by term.

Let:

$$f(t) = a_0/2 + \Sigma a_k \cos k\omega t + b_k \sin k\omega t \quad (\forall t \in R) \tag{A1}$$

Equation 9 can be rewritten as follows:

$$N(t) = N_0 \exp(rt)/(1 + rN_0\, I(t)) \tag{A2}$$

where

$$I(t) = \int_0^t f(t) \exp(rt')\, dt' \tag{A3}$$

By substituting Eq. A1 into Eq. A3 and integrating, one obtains:

$$I(t) = a_0(\exp(rt) - 1)/2r + \sum_1^{\infty}(k\omega b_k - ra_k)/(r^2 + k^2\omega^2) + \exp(rt) \times \sum_1^{\infty}\left[(ra_k - k\omega b_k)\cos k\omega t + (k\omega a_k + rb_k)\sin k\omega t)\right]/(r^2 + k^2\omega^2) \tag{A4}$$

Substitution of Eq. A4 into Eq. A2 gives the explicit solution. Assume that the Fourier series contains a finite number, n, of terms different from zero. Then, because:

$$\sum_1^{n}(k\omega b_k - ra_k)/(r^2 + k^2\omega^2) = M < \infty$$

the following asymptotic value is obtained:

$$r\exp(-rt)I(t) \approx a_0/2 + \sum_1^{n} r\left[(ra_k - k\omega b_k)\cos k\omega t + (k\omega a_k + rb_k) \times \sin k\omega t\right]/(r^2 + k^2\omega^2)$$

It follows that for large times the population, in the two cases, is approximately given by:

Case 1: $r \ll \omega$

$$N(t) \approx \left[\frac{1}{T}\int_0^T f(t)\, dt\right]^{-1} \tag{A5}$$

Case 2: $r \gg \omega n$

$$N(t) \approx 1/f(t) = K(t) \tag{A6}$$

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