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Stocking effects on asymmetrical population growth under delayed regulation*

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Abstract: The constant rate stocking effects are considered on the population with delayed asymmetrical growth. The stocking increases the equilibrium level of the population. If the asymmetrical parameter is large, the stocking produces instability of the equilibrium. Contrarily, if it is small, the stocking produces stability. The constant rate harvesting has contrary effects to that of the stocking. The proportional harvesting has a stabilizing effect on the system. The stocking is an effective way for controlling natural populations.

1. Introduction

The asymmetrical population growth is known to occur in the case that the density dependence is not linear to the population density. Recent evidence reveals that it is an important factor to describe the population dynamics (PELLA and TOMLINSON, 1969; GILPIN and AYALA 1973; FLETCHER, 1978; THOMAS *et al.*, 1980; MUELLER and AYALA, 1981). Such a growth is formulated as,

$$\frac{dP(t)}{dt}=r\left[1-\left\{\frac{P(t)}{K}\right\}^{\theta}\right]P(t), \quad (1)$$

where r, K and θ denote intrinsic growth rate, saturation level, and the parameter of asymmetry, respectively. The $P(t)$ denotes the population size at time t. Still more, the growth of a given population is often regulated by the past population size (NICHOLSON, 1954; MORAN, 1959; MAYNARD SMITH, 1968). The dynamics of the population with time lag regulation is studied for fishing effects (WALTER, 1973), and stability of the equilibrium (JONES, 1962a, b; KAPLAN and YORKE, 1975; HADELAR, 1976; STECH, 1978). The simple delayed logistic model proposed by HUTCHINSON (1948) is,

$$\frac{dP(t)}{dt}=r\left\{1-\frac{P(t-\tau)}{K}\right\}P(t), \quad (2)$$

where τ is time lag and $P(t-\tau)$ is the population size at time $t-\tau$. This equation is analyzed by MAY (1973, 1976) and MAYNARD SMITH (1974).

Another factor for which more theoretical studies are needed is that of population dynamics with stocking. In actual cases of sea farming, it has been common to stock natural population with juveniles reared from eggs. This paper introduces an analysis made of the asymmetrical population growth under delayed regulation with special reference to the case in which the stocking takes place.

2. Model and its analysis

The asymmetrical logistic population growth under delayed regulation together with harvesting and stocking treatments is described as,

$$\frac{dP(t)}{dt}=r\left[1-\left\{\frac{P(t-\tau)}{K}\right\}^{\theta}\right]P(t)+R-f, \quad (3)$$

where R is the stocking rate and f the harvesting function. Assuming the harvesting rate to be constant ($f=H=$constant), when $dP/dt=0$, the equilibrium level P^* is the value which satisfies the following equation;

$$P^{*\theta+1}-K^{\theta}P^*-\frac{K^{\theta}}{r}(R-H)=0. \quad (4)$$

When neither harvesting nor stocking occur or $R-H=0$, the equilibrium level is K. If $f=hP(t)$, where $h=$constant, the equilibrium level P^* is the value which satisfies the following equation;

$$P^{*\theta+1}-\left(1-\frac{h}{r}\right)K^{\theta}P^*-\frac{K^{\theta}}{r}R=0. \quad (5)$$

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Stability of the equilibrium

The local stability of the equilibrium is determined by the neighborhood stability analysis. Denoting a small perturbation from the equilibrium by x, the population density is represented by as $P(t)=P^*+x(t)$. Differentiating both sides by t, we get $dP(t)/dt=dx(t)/dt$. Substituting this into equation (2), we get

$$\frac{dx(t)}{dt}=r\left[1-\left\{\frac{P^*+x(t-\tau)}{K}\right\}^{\theta}\right]\times\{P^*+x(t)\}+R-f. \quad (6)$$

Taylor expanding the $\{\ \}^{\theta}$ term, and neglecting 2nd and higher order terms of x, we get the following equation for $f=H=$constant:

$$\frac{dx(t)}{dt}=r\left[\left\{1-\left(\frac{P^*}{K}\right)^{\theta}\right\}x(t)-\theta\left(\frac{P^*}{K}\right)^{\theta}x(t-\tau)\right]. \quad (7)$$

When $R-H=0$ or $R=H=0$ (in these cases, $P^*=K$),

$$\frac{dx(t)}{dt}=-r\theta x(t-\tau)\,. \quad (8)$$

If time is measured in units of τ, then

$$\frac{dx(t)}{dt}=-r\tau\left[\left\{\left(\frac{P^*}{K}\right)^{\theta}-1\right\}x(t)+\theta\left(\frac{P^*}{K}\right)^{\theta}x(t-1)\right]. \quad (9)$$

Putting $a=r\tau\{(P^*/K)^{\theta}-1\}$ and $b=r\theta\tau(P^*/K)^{\theta}$, the equation becomes

$$\frac{dx(t)}{dt}=-ax(t)-bx(t-1)\,. \quad (10)$$

When $R-H=0$, $a=0$ and $b=r\theta\tau$. The equilibrium is stable if

$$r\theta\tau<\pi/2\,, \quad (11)$$

and unstable if

$$r\theta\tau>\pi/2\,. \quad (12)$$

When $f=hP(t)$, the local stability is determined by

$$\frac{dx(t)}{dt}=-r\left[\left\{\left(\frac{P^*}{K}\right)^{\theta}+\frac{h}{r}-1\right\}x(t)+\theta\left(\frac{P^*}{K}\right)^{\theta}x(t-\tau)\right]. \quad (13)$$

Measuring time by τ, we get

$$\frac{dx(t)}{dt}=-r\tau\left[\left\{\left(\frac{P^*}{K}\right)^{\theta}+\frac{h}{r}-1\right\}x(t)+\theta\left(\frac{P^*}{K}\right)^{\theta}x(t-1)\right]. \quad (14)$$

Putting $a=r\tau\{(P^*/K)^{\theta}+h/r-1\}$ and $b=r\theta\tau(P^*/K)^{\theta}$, this equation is expressed in the same manner as equation (10). When $R=0$, the equilibrium is stable if

$$1-\frac{\pi}{2\theta\tau}<\frac{h}{r}<1. \quad (15)$$

and unstable if

$$\frac{h}{r}<1-\frac{\pi}{2\theta\tau}\ \text{or}\ h>r. \quad (16)$$

When $r-h<0$, the population becomes extinct.

3. Stocking effects

The case of $f=H=$constant

Assuming $r\tau=$constant, the stocking effects are given as follows. If R increases, the parameters a and b increase as

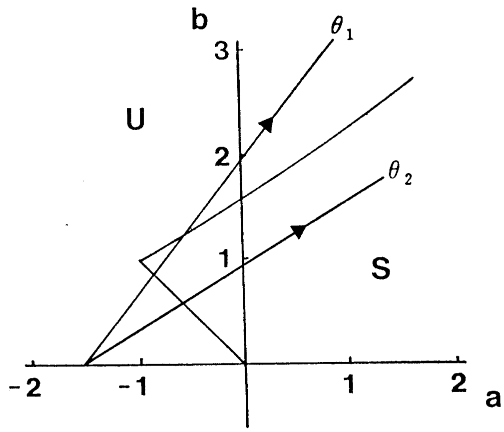

Fig. 1. Stocking effects on the system described by equation (3) (see text) under the condition of constant-rate harvesting ($f=H$). Increase of stocking carries the point rightward along the $b=\theta\ (r\tau+a)$ line. Arrow shows the direction to which the initial point moves by stocking. The constant-rate harvesting carries the point to the contrary direction to that in the stocking. Stability domains are calculated by MAYNARD SMITH (1974). S, stable region. U, unstable region. See text for symbols a, b, θ_1 and θ_2.

$$b=\theta(r\tau+a), \quad b>0. \qquad (17)$$

The gradient of the straight line (17) depends on the parameter θ, as indicated in Fig. 1. If $\theta_1>\theta_2>0$, the gradient θ_1 is steeper than that of θ_2. If θ is large, the stocking affects strongly the stability of the equilibrium, and produces instability. Contrarily, if θ is small, the stocking ensures the equilibrium to be stable (Fig. 1). The harvesting has a contrary effect to that of stocking.

The case of $f=hP(t)$

In this case, the relation between a and b is,

$$b=\theta\{(r-h)\tau+a\}, \; b>0. \qquad (18)$$

If $(r-h)\tau=$constant, the stocking effects on the stability of the equilibrium are similar to the above-mentioned case ($f=H=$constant). The harvesting decreases the height of the line (18). It means that the sufficient harvesting produces stability (here assumed $r>h$) (Fig. 2).

When $\theta\neq1$, the asymmetrical population growth occurs. It provides the various effects on the system. In the practical operation of controlling natural populations, these effects must be taken into consideration. In some cases, the stocking produces serious effects on the population dynamics (WATANABE, 1983, 1986, 1987, 1988). In the present study, it is clarified that the stocking plays a very important role in the time-delayed asymmetrical population growth. It seems to be reasonable that the stocking is effective for controlling natural populations.

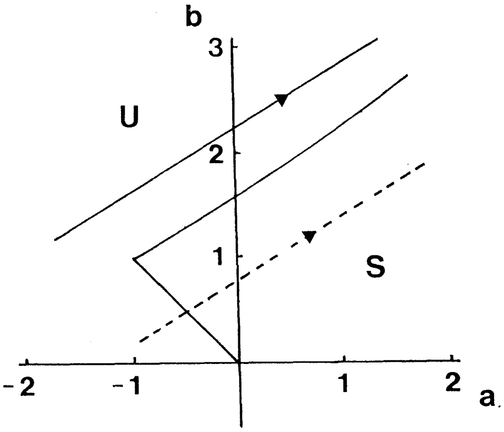

Fig. 2. Stocking effects on the system described by equation (3) (see text) under the condition of proportional harvesting ($f=hP$). Increase of stocking carries the point rightward along the $b=\theta$ $\{(r-h)\tau+a\}$ line. Arrow shows the direction to which the initial point moves by stocking. Dotted line shows the harvesting effect on the system. Harvesting downs the line parallel to the initial one. θ changes the gradient of the line. Cf. Fig. 1 for symbols.

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時間遅れのある非対称生長を示す個体群に対する放流の影響

渡 邊 精 一

要旨: 個体群が時間遅れのある非対称生長を示すとき，一定率の放流が個体群に与える影響を考察した。個体群生長の非対称性を示すパラメタの値が大きいとき，放流によって個体群の平衡点は不安定化する。逆に，そのパラメタが小さいときには放流は平衡点の安定化をもたらす。一定率の漁獲は放流とは逆の影響を個体群に与える。個体数に比例して漁獲する場合は，漁獲により個体群の平衡点は安定化する傾向にある。したがって，放流は資源を管理する有効な一手段であるといえる。