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AND THE VON FOERSTER EQUATION**

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DYNAMICS OF POPULATIONS OF BIOMPHALARIA GLABRATA
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F.A.B. Coutinho* and A.B. Coutinho**

ABSTRACT

Changes in time of populations of *Biomphalaria Glabrata* due to changes in the rate of infection by *Schistosoma Manson* are investigated. This is done by applying von Foerster equations with boundary conditions derived from experiment. The resulting equation is solved in some simplified cases and applications of the formalism to ecological control is suggested.

I - INTRODUCTION

In a previous paper (Coutinho, 1968) we have proposed a model to describe populations of *Biomphalaria glabrata* in steady state. In this model the population is described by two parameters, namely, the rate of infection by trematodes p , and the biomass density of the habitat M .

In the present paper we want to show that variations of the population with time due to variations in p with M constant can be described within the framework of the previous model by means of the use of the so called Von Foerster Equation.

The content of the paper is as follows. In section II we describe briefly the stationary model together with the simplifying assumptions made about the population. In section III the Von Foerster Equation is described and applied to the problem of representing the variation of the population in time for a given

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variation of p and finally the equation is solved in simple cases. In conclusion in the section IV it is shown how the Von Foerster Equation can be applied to more general problems in the dynamics of the Biomphalaria glabrata's populations.

The Biomphalaria glabrata is the intermediate host of the Schistosoma mansoni. The use of poison to control the populations of snails presents difficulties and damages the natural environment. This paper is particularly concerned with how to evaluate ecological methods of control.

II - THE STATIC MODEL

Let $N_T dT$ be the number of snails per unit area of the habitat, in a steady state population of Biomphalaria glabrata whose age is between T and $T+dT$. We are interested in populations where the external causes of death, which are age independent, add up to a high death rate. The habitat is assumed to be in steady state, that is, producing a certain amount of food per unit time which is constant in time and hence characterized by a Biomass density M .

It was shown previously (Coutinho - 1968) that such a population of Biomphalaria glabrata can be described by the equations below and whose physical meaning will be explained immediately afterwards:

$$N_T dT = N_0 e^{-\lambda T} dT + \mathfrak{F}(T) dT \quad (1)$$

where

$$N_0 = \frac{M}{\mathcal{L}_\lambda \{m(T)\}} \quad \mathcal{L}_\lambda \{m(T)\} = \int_0^\infty e^{-\lambda T} m(T) dT$$

Here $\mathfrak{F}(T)$ is different from zero only in the neighbourhood of

the age $T=0$ (see Fig. I) and $m(T)$ gives the mass of the snail at the age T .

The physical meaning of the formulae is the following. Since the causes of death by external factors are very large, we assume that those causes determine entirely the shape of the age distribution curve, except in the neighbourhood of the age $T=0$. In this region the death rate increases very much and so the incredibly excessive birth rate evident in populations of Biomphalaria glabrata is curbed. On the other hand, as shown in Coutinho (1968), the excessive birth rate assure us that if the population is in steady state then the mass of the population per unit area equals the biomass density of the habitat. So, as in Eq. 1, the total population was divided into two parts. One part has the age distribution shape determined by the external causes of death and the total mass determined by the habitat. The other part is composed by very young individuals and is due to the fact that the birth rate is excessive.

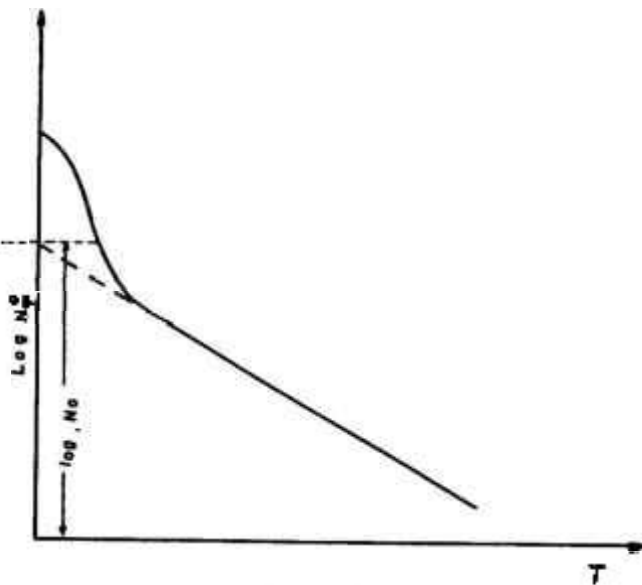


Figure I

This model, crude as it is, explains two phenomena observed in populations of Biomphalaria glabrata living in small lakes and permanent ponds. In fact it follows from Eq. 1, that the maximum age attainable in a given population is inversely proportional to λ

$$T_c = \frac{-\log \alpha}{\lambda} \quad (2)$$

where α is a number $0 < \alpha < 1$.

But on the other hand λ is related to the rate of infection by trematodes p by

$$\lambda = D(p + m - mp) \quad (3)$$

where D is a constant and m is the rate of all other causes of death lumped together. From Eq. 3 and Eq. 2 it follows

$$T_c = \frac{\frac{-\log \alpha}{D(1-m)}}{p + \frac{1}{1-m}} \quad (4)$$

Since the diameter of the snails D , is proportional to age (Barbosa - 1951) for the values encountered in our experimental data, it follows that the maximum diameter D_{\max} which can be found in the population is related with the value of p by

$$D_{\max} = \frac{\frac{-a \log \alpha}{D(1-m)}}{p + \frac{m}{1-m}}$$

This relationship was observed experimentally (Coutinho - 1961a).

The second consequence is that the population density

N varies with λ as follows

$$N_1 = \frac{M}{\mathcal{L}_\lambda\{m'(T)\} + m(0)} \quad (5)$$

where $\mathcal{L}_\lambda\{m'(T)\} = \int_0^\infty e^{-\lambda T} \frac{dm(T)}{dT} dT$. Since $\mathcal{L}_\lambda\{m(T)\} \rightarrow 0$ as

$\lambda \rightarrow \infty$, N_1 increases with λ . This has also been observed (Coutinho - 1961b).

A practical consequence of this behaviour is an ecological method of control of the Biomphalaria glabrata populations. We shall return to this in section III of this paper.

The model was also applied to populations of Biomphalaria glabrata living in rapid flowing channels and small rivers (Coutinho - 1970) with good qualitative results.

III - THE VON FOERSTER EQUATION

The Von Foerster Equation was invented in 1959 (Von Foerster - 1959) to describe self-sustained populations of cells. A very detailed study of this equation can be found in an article by Trucco (1965a and 1965b).

If $n(t,T)dT$ is the number of organisms whose age is between T and $T+dT$ at a certain time t , then the Von Foerster equation is

$$\frac{\partial n(t,T)}{\partial t} + \frac{\partial n(t,T)}{\partial T} = -\lambda(t,T,\dots) n(t,T) \quad (6)$$

In this equation $\lambda(t,T,\dots)$ is a function, known as loss function, and in the general case depends on t , T , and possibly on $n(t,T)$ and any other parameter characterizing the system.

In the same spirit of the model presented in section II, we assume that the bulk of the causes of death in our population of Biomphalaria glabrata are external causes which act independently of the age of the animal. We are concerned in this paper with knowing what happens with the population when those causes of death change with time, say from $\lambda_1 = \lambda(0)$ to $\lambda_2 = \lambda(t=t_1)$. Again our population will be divided in two parts. One of these parts is composed of very young animals. The other part, whose age distribution curve is determined by external causes, has the total mass equal to the maximum mass of organisms which can live continuously in the habitat in study. We shall assume that this second part of the population evolves accordingly to the Von Foerster Equation and that its total mass equals the maximum. This means that the total mass equals the biomass density of the habitat at any time t . We shall call this part of the population $n_1(t, T)$. This is reasonable if the habitat is not changing with time and if we have only small discontinuous changes of mortality or slow continuous changes. In practical situations we are interested in this last condition, although in this paper we are going to treat only the case of small discontinuities.

We can then write:

$$\int_0^{\infty} n_1(t, T) m(t, T) m(T) dT = M \quad (7)$$

To see that the equations (6) and (7) together, have a well determined solution, we note that in the case where $\lambda(t, T, \dots)$ doesn't depend on $M(t, T)$ (Trucco - 1965a, 295 ff) we have

$$M_1(t, T) = \alpha(t-T) \exp \left[- \int_{x=0}^T \lambda(t-T+x, x) dx \right] \quad \text{for } t > T \quad (8a)$$

$$M_1(t, T) = \beta(T-t) \exp \left[- \int_{x=T-t}^T \lambda(t-T+x, x) dx \right] \quad \text{for } t < T \quad (8b)$$

where $\alpha(t) = M_1(t, 0)$ and $\beta(T) = M(0, T)$

We know $\beta(T) = M_1(0, T)$ from Coutinho (1968) and it is:

$$\beta(T) = \frac{M}{\mathcal{L}_{\lambda_1}\{m(T)\}} e^{-\lambda_1 T} \quad \text{where} \quad \lambda(0, T) = \lambda_1.$$

We have supposed $\lambda(t, T, \dots) = \lambda(t, T)$ that is, function only of t and T , and we shall suppose that this function is known. We shall comment on this in the following section.

If we substitute equation (8a) and (8b) in the equation (7) we find:

$$M = \int_0^t \alpha(t-T) \exp \left[- \int_{x=0}^T \lambda(t-T+x, x) dx \right] m(T) dT + \int_t^\infty \frac{M}{\mathcal{L}_{\lambda_1}\{m(T)\}} e^{-\lambda_1 T} \exp \left[- \int_{x=T-t}^T \lambda(t-T+x, x) dx \right] m(T) dT \quad (9)$$

Call $m(T) \exp \left[- \int_{x=0}^T \lambda(t-T+x, x) \right] = K(t, T)$

and $E(t) = \int_t^\infty \frac{M}{\mathcal{L}_{\lambda_1}\{m(T)\}} e^{-\lambda_1 T} \exp \left[- \int_{x=T-t}^T \lambda(t-T+x, x) dx \right] m(T) dT$

Then equation (9) becomes

$$M = \int_0^t \alpha(t-T) K(t, T) dT + E(t) \quad (10)$$

Equation (10) is a Volterra Integral equation of the first kind. The solution of (10) determines completely the equation (8a).

To exemplify let us take a very simplified case. Let us suppose that $\lambda(T)$ is in fact a step function, that is:

. 8 .

$$\begin{aligned} \lambda(t) &= \lambda_1 & \text{for } t < 0 \\ \lambda(t) &= \lambda_2 & \text{for } t > 0 \end{aligned}$$

The equations (8a) and (9a) reduces respectively to

$$M(t, T) = \alpha(t-T) e^{-\lambda_2 T} \quad \text{for } t > T \quad (11a)$$

$$M(t, T) = \frac{M}{\mathcal{L}_{\lambda_1}\{m(T)\}} e^{-\lambda_1(T-t)} e^{-\lambda_2 T} \quad \text{for } t < T \quad (11b)$$

and equation (9) reduces to:

$$M = \int_0^T \alpha(t-T) e^{-\lambda_2 T} m(T) dT + \frac{M}{\mathcal{L}_{\lambda_1}\{m(T)\}} e^{-(\lambda_2 - \lambda_1)t} \int_t^{\infty} e^{-\lambda_1 T} m(T) dT \quad (12)$$

Instead of solving equation (12) for a general $m(T)$ we shall first examine the behaviour of the solution for large values of t and then solve the equation in two simple cases.

Suppose:

$$m(t) = \sum_{n=0}^q m_n T^n$$

Then

$$\int_t^{\infty} e^{-\lambda_1 T} m(T) dT = \sum_{n=0}^q m_n \left[\frac{e^{-\lambda_1 t}}{\lambda_1^{n+1}} \left[(\lambda_1 t)^n + n(\lambda_1 t)^{n-1} + n(n-1)(\lambda_1 t)^{n-2} + \dots + n! \right] \right]$$

So (12) becomes:

$$M = \int_0^t \alpha(t-T) e^{-\lambda_2 T} m(T) dT + \frac{M e^{-\lambda_2 t}}{\mathcal{L}_{\lambda_1}\{m(T)\}} \sum_{n=0}^q m_n \left[\frac{1}{\lambda_1^{n+1}} \left[(\lambda_1 t)^n + n(\lambda_1 t)^{n-1} + \dots + n! \right] \right]$$

as $t \rightarrow \infty$ this reduces to:

$$M = \int_0^t \alpha(t-T) e^{-\lambda_2 T} m(T) dT$$

Taking Laplace transforms one gets

$$\bar{\alpha}(s) = \frac{M}{s \int_0^{\infty} \{e^{-\lambda_2 T} m(T)\}} = \frac{M}{s \bar{m}(s+\lambda_2)}$$

where

$$\bar{m}(s) = \int_0^{\infty} e^{-sT} m(T) dT \quad \text{and} \quad \bar{\alpha}(s) = \int_0^{\infty} e^{-st} \alpha(t) dt$$

but $\lim_{s \rightarrow 0} s \bar{\alpha}(s) = \lim_{t \rightarrow \infty} \alpha(t)$ and hence

$$\lim_{t \rightarrow \infty} \alpha(t) = \frac{M}{\bar{m}(\lambda_2)} = \frac{M}{\int_0^{\infty} \{e^{-\lambda_2 T} m(T)\}} \quad (13)$$

This result agrees with what one should expect from the static model described in section II.

Now let us consider the solution of the equation (12), for two special forms of $m(T)$, namely $m(T) = m_0$ and $m(T) = m_0 + m_1 T$. Of course these two simple forms does not fit the real $m(T)$ for the Biomphalaria glabrata. We are nevertheless working out solutions in those two cases because of certain features we want to discuss.

We find for the case $m(T) = m_0 + m_1 T$ that

$$\alpha(t) = C e^{-bt} + \frac{A\lambda_2}{b} \left[1 - e^{-bT} \right]$$

where

$$C = A - B, \quad A = \frac{M\lambda_2}{m_0}, \quad B = \frac{M}{\frac{m_0}{\lambda_1} + \frac{m_1}{\lambda_1^2}} \frac{m_1}{\lambda_1 m_0} \quad \text{and} \quad b = \lambda_2 + \frac{m_1}{m_0}$$

when $m = 0$ we get the case $m(T) = m_0$

$$\alpha(t) = \frac{M}{\mathfrak{L}_{\lambda_2}\{m(T)\}}$$

Let us discuss the solution in the simpler case $m(T) = m_0$. In this case the equations (11a) and (11b) reduce to

$$M_1(t, T) = \frac{M}{\mathfrak{L}_{\lambda_2}\{m(t)\}} e^{-\lambda_2 T} \quad \text{for } t > T \quad (14a)$$

$$M_1(t, T) = \frac{M}{\mathfrak{L}_{\lambda_1}\{m(t)\}} e^{-\lambda_1(T-t)} e^{-\lambda_2 t} \quad \text{for } t < T \quad (14b)$$

The equations (14a) and (14b) are represented in three different times $t=0$, $t=t_1$ and $t=\infty$ for $\lambda_1 > \lambda_2$ in Fig. II and for $\lambda_1 < \lambda_2$ in Fig. III.

Physically the two processes are described in the following way. Take the case $\lambda_1 > \lambda_2$ (Fig. II) first. Before $t = 0$ among a huge number born per unit time (dashed line in the figures) only a number $\frac{M}{\mathfrak{L}_{\lambda_1}\{m(T)\}}$ of snails per unit time is able to reach old age. The other have been eliminated at very early ages. At $t=0$ the mortality decreases suddenly and so more and more snails are reaching greater lifespans and as consequence less and less food is left to the younger ones. Because of this the number of the snails at the age $T=0$, which has a chance to reach greater ages begins to decrease, that is, the mortality at low ages begins to increase. In our examples this occurs suddenly because we have assumed that λ_1 changes suddenly in λ_2 at $t=0$. In practice this occurs slowly. In the case of $\lambda_1 < \lambda_2$ (Fig. III) since the mortality due to external causes increases at $t=0$, more and more food is being made available and so the mortality at very young ages decreases.

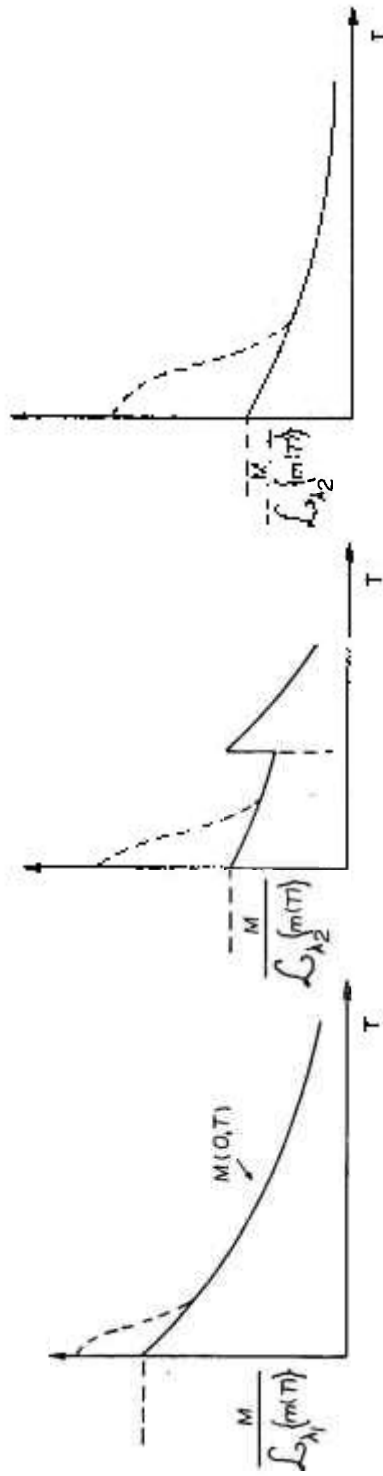


Figure II

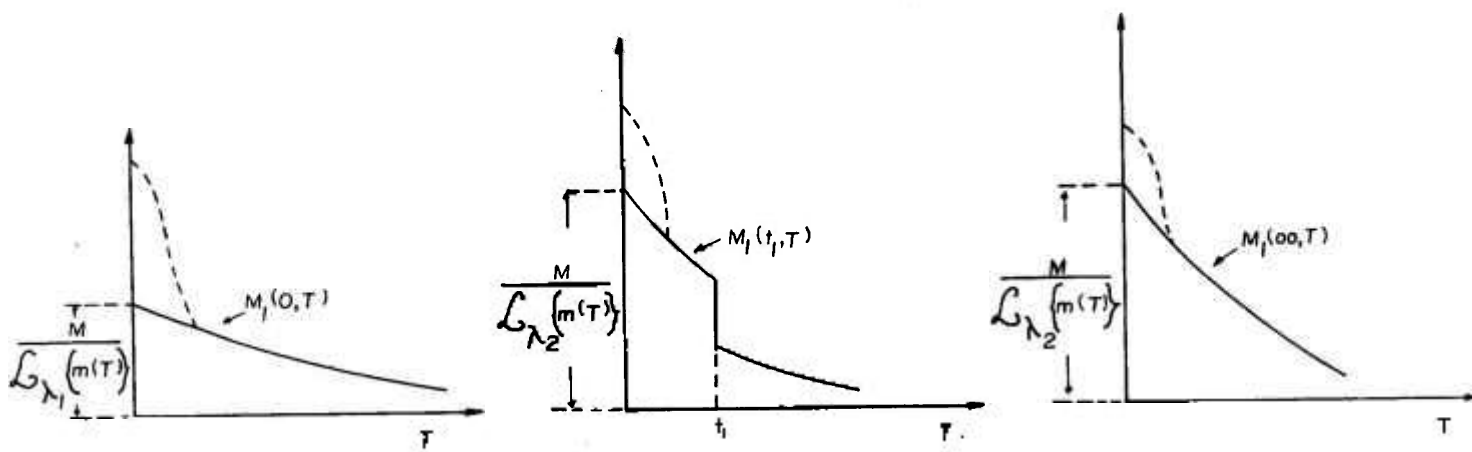


Figure III

Equations (14a) and (14b) and the considerations we have just made show that if the population is not in steady state, the relationship between the maximum diameter and the rate of infection by trematodes (Equation (4) in this paper) can be violated. In a previous paper (Coutinho, 1963) both cases $\lambda_1 > \lambda_2$ and $\lambda_1 < \lambda_2$ were described as "populatio in statu moriendi" and "populatio in statu nascendi", respectively.

IV - APPLICATIONS

In this section we describe two possible applications of the formalism, both concerned with the viability of methods of control of the populations of Biomphalaria glabrata.

It was shown in (Coutinho - 1968) that there is a limit to the infection rate that the populations of Biomphalaria glabrata can sustain. The first method consists then in raising the infection rate by trematodes by artificially increasing the number of definitive hosts in contact with the Biomphalaria population we want to control (Coutinho - 1961a).

The formalism described above can be used, at least in principle, to calculate the final infection rate in the population of Biomphalaria glabrata when the population of definitive hosts has been raised artificially by a known amount. The problem is complicated since it involves three populations: the populations of definitive hosts, the population of intermediate hosts (Biomphalaria glabrata) and the populations of sundry species of parasites. The fact that in general the definitive host does not die because of the infection, simplifies things quite a lot, both from the theoretical and practical points of view. Indeed, because of this the change in the definitive host populations can be considered as an known input datum.

The final answer depends on both easily measurable parameters and some others that will require a huge amount of experimental work. As examples of easily measurable parameters there is the average number of parasites per definitive host, the fecundity of the parasites, etc. One parameter hard to measure is the probability of infection of both the definitive host or the intermediate host, the Biomphalaria glabrata.

The second method was proposed recently by C.S. Richards (1970). He discovered strains of snails which are immune to certain strains of Schistosoma mansoni. He has raised three kinds of snails classified with respect to their susceptibility to the puerto-rican Schistosoma mansoni. Susceptible at any age, juvenile susceptible at any age, juvenile susceptible but adult refractory and refractory at any age. The variation in mortality with age in the case of snails juvenile susceptible but adult refractory can be easily incorporated in our treatment both in the stationary case as in the dynamic case described in this paper. The method of control proposed consists in introducing into the population of Biomphalaria glabrata snails which are immune to the particular strain of Schistosoma mansoni in the region.

The formalism can be used to calculate how long it would take for the population to shift completely to insusceptibility. The final answer will depend in one parameter which is very hard to measure, namely, the coefficient of self-fecondation (Coutinho - 1957).

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RESUMO

Os efeitos de mudanças na taxa de infecção por Schistosomose Mansonica em populações de Biomphalaria Glabrata são estudados. Isto é feito aplicando as equações de Von Foerster com condições de contorno tiradas de estudos experimentais. As equações são resolvidas em casos simples e aplicações do formalismo ao controle ecológico são sugeridas.

RÉSUMÉ

Dans ce travail sont étudiés les effets de changes du taux d'infection par Schistosoma Manson dans les populations de Biomphalaria Glabrata. Cela est fait en appliquant les équations de Von Foerster avec des conditions de contour tirées expérimentalement. Les équations résultantes sont résolues pour des cas simples. En même temps, sont suggérées applications du formalisme au control écologique.

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