SNAIL POPULATION IN RUNNING WATER

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A model developed in a previous paper (Coutinho and Coutinho, *Bull. Math. Biophysics*, **30**, 553–563, 1968) is used to study populations of *Biomphalaria glabrata* in fast-flowing rivers and channels. The results obtained are in good qualitative agreement with the phenomena experimentally observed, and suggest that the use of artificial channels can be a very useful tool for the experimental study of some important aspects of the ecology of the *Biomphalaria glabrata*.

Biomphalaria glabrata is a planorbid snail found in fresh water collections of the neotropical region. As usual among snails, it harbors the larval stage of the life cycle of several trematode flatworms which parasitize vertebrate animals including man, but the adult stages of the majority of these larvae are yet to be identified. Among the identified parasites are, for instance, the larvae of *Halipegus dubius* whose definitive host is the frog *Leptodactylus ocellatus* and those of the *Schistosoma mansoni* which parasitizes man, producing a serious and widespread disease—the mansonic bilharziosis—one of the last uncontrolled great endemics. Of course, larval trematode infection in the snail is a serious and lethal disease.

In a previous paper (Coutinho and Coutinho, 1968) which we shall call (I), we have studied the effects of the larval trematode infection rate in the *Biomphalaria* snail populations. With the help of a rather schematic formal model, it was possible to calculate both the age structure and the population density, using the trematode infection rate and the biomass density as parameters characterizing the habitat. It was also shown that there is an upper bound for the trematode infection rate above which the snail population can no longer reach the steady state described in (I). This steady state will subsequently be called saturating equilibrium.

The existence of this upper bound is important because the bilharzian endemics only reach calamity levels when the snail populations exist in the optimum conditions which permit the maintenance of the saturating equilibrium. This concurs with the fact already noticed by Mozley (1954) that the sites of prosperous planorbid populations are located in areas where human occupation evicted the superior wild fauna. The scarcity of vertebrate animals harboring the adult stage of trematodes favors the advent of the saturating equilibrium as a result of the lowering of the snail infection rates. Conversely, the return to undisturbed natural conditions will re-establish the parasitic control of the snail population, reducing its numbers to its natural scarcity.

These results led us to suggest an entirely ecological way to control the snail populations. It would consist of breeding animals liable to infection by the trematodes which, when in larval stage, infest the *Biomphalaria glabrata*. Trematodes, unless extremely numerous in their vertebrate host, seldom kill it, as opposed to what we observe among snails, where, as remarked before, the trematode infection is frequently mortal. Therefore, the infection rate in the intermediate hosts, i.e., their death rate, is directly proportional to the number of definitive hosts in the same habitat. Hence, the rearing of only one species of trematode-bearing vertebrate host is expected to promote the increase of the infection rate of the snails enough to avoid the saturating equilibrium.

These claims are valid for snails breeding in still-water sites—lakes, ponds—or waterways sluggish enough to behave as lakes. The conditions present in swift-flowing streams are different. In this case where the flow is strong enough to carry the snails downstream, the formalism must be altered in order to account for the new conditions.

This paper intends to study the conditions that must be satisfied in swift-flowing rivers or channels in order to maintain a saturating population of *Biomphalaria glabrata*. It will be shown that these conditions are much more stringent than those prevailing in lakes.

It is possible, as we shall see, to reach good quantitative results, in spite of the mathematical complications which the problem creates. These results have

practical importance in the planning of artificial channels and waterways. They also confirm the mathematical model presented in (I).*

Let us consider a snail population in a steady state in a swift-flowing channel. Let l be a curvilinear abcissa traced along the channel. We will suppose that the velocity of the stream in the channel will not change with time. This hypothesis is consistent with the assumed steadiness of the snail population.
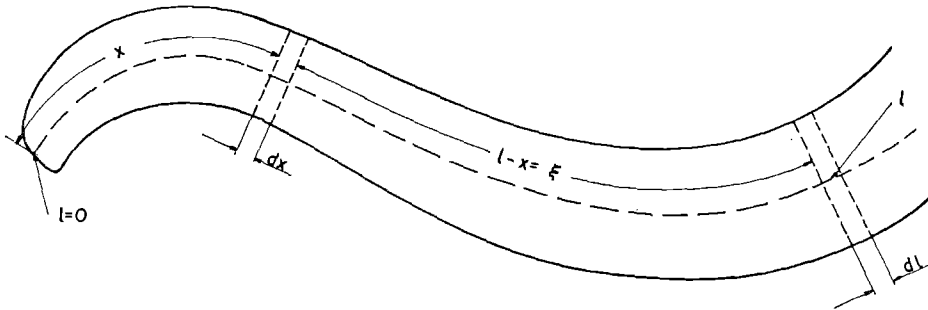

Figure 1.

Let $N_{T,l}\, dl\, dT$ be the number of snails aged between T and $T + dT$ located between l and $l + dl$ in the channel. This number does not change with time because the population is supposed to be in a steady state. Let us suppose that at a certain time, $t = 0$, we tag with an identifying mark all the snails in the channel whose age is between T_0 and $T_0 + dT$. Their number between l and $l + dl$ at $t = 0$ is, of course, $N_{T_0 l}\, dT\, dl$ and it will vary with time. Let us call $C(t, l)\, dl\, dT$ their number at time t. As the population is in steady state, we will have

$$C(t, l) = N_{T,l} \quad \text{for} \quad T = T_0 + t. \tag{1}$$

During an elementary interval ∂t, $C(t, l)\, dl\, dT$ decreases through the agency of

(i) death—a certain fraction $\lambda(t, l)C(t, l)\, dl\, dT\, \partial t$ of the snails dies,
(ii) removal—a certain fraction $a(t, l)C(t, l)\, dl\, dT\, \partial t$ is swept away by the stream and will be stranded in sites downstream of l.

The total decrease from both causes in a time ∂t is, of course,

$$-\{\lambda(t, l) + a(t, l)\}C(t, l)\, dl\, dT\, \partial t.$$

* There are a few errors in this paper which however do not alter the conclusions. In equation (7) and the following, D_1 should be replaced by $1/D_1$. In addition, in equation (7), $1/(1 - m)$ should be replaced by $m/(1 - m)$. In the third equation in page 558 the term $k_2[dm(T)/dT]\, dT$ should read $k_2[dm(T)/dT]\, dt$. There is a λ missing in front of the last term of the last equation of page 561 and finally the denominator of the last expression should read $L_\lambda[m'(T)] + m(0)$.

The population in the region between l and $l + dl$ is maintained also by the arrival of snails swept from regions upstream.

Let $P(x, \xi)$ be the probability of a snail swept from a point x in the channel to be stranded for the first time in a point located between x and $x + \xi$. Then $[\partial P(x, \xi)]/\partial \xi \, d\xi$ is the probability that the displacement terminates between $x + \xi$ and $x + \xi + d\xi$. Of course, we have $P(x, \infty) = 1$ and $P(x, 0) = 0$. Therefore,

$$\int_0^\infty \frac{\partial P(x, \xi)}{\partial \xi} \, d\xi = 1.$$

We shall assume that the velocities of transport are fast enough so that one can neglect the time spent during the transport in comparison with the lifespan of the snails. We know, therefore, that the number of snails added to $C(t, l) \, dl \, dT$ in a time interval ∂t, coming from regions between x and $x + dx$, will be

$$a(t, x) \frac{\partial P(x, \xi = l - x)}{\partial \xi} \, C(t, x) \, dx \, dT \, dl \, \partial t.$$

Therefore, we can write

$$\frac{\partial C(t, l)}{\partial t} = -[\lambda(t, l) + a(t, l)]C(t, l) + \int_0^l a(t, x) \frac{\partial P(x, \xi = l - x)}{\partial \xi} \, C(t, x) \, dx. \quad (2)$$

Even if $\lambda(t, l)$, $a(t, l)$ and $[\partial P(x, \xi)]/\partial \xi$ are given, (2) can only be solved by numerical methods. Nevertheless, as we shall see, it is possible to introduce certain simplifications and arrive at an analytical solution.

First, it is possible to write $a(t, l) = a(l)$ because the velocity of the stream was supposedly constant in time and any influence of the individual snail's size in the probability of being swept downstream is necessarily small and may be neglected.

Second, we shall suppose $a(l) = a$, and $P(x, \xi) = P(\xi)$. These two simplifications imply a very uniform channel. They cannot be accepted in the case of rivers or natural waterways, but can be accepted in the case of artificial ditches and drains. We shall return to this matter at the end of the paper.

We shall suppose that $\lambda(t, l) = \lambda(t)$, again implying a very uniform channel. Naturally, λ depends on the age T and therefore is a function of t. Nevertheless, the death rate due to larval trematode infection, which is independent of the snails age, is very high in the cases with which we are concerned. We can suppose, then, that trematode infection dominates any other age-dependent cause of death, except in the neighborhood of age zero, where empirical observation shows a great increase in mortality rates. Because of this, as discussed in (I), one can choose the age T_0 of (1), so that for $T > T_0 \lambda(t) = \lambda$, that is, independent of T.

Equation (2) can therefore be written in the form

$$\frac{\partial C(t, l)}{\partial t} = -(\lambda + a)C(t, l) + a \int_0^l \frac{dP(\xi = l - x)}{d\xi} C(t, x) \, dx. \tag{3}$$

Equation (3) can be analytically solved, by use of Laplace transform methods, and the solution is found to be

$$C(t, l) = e^{-(\lambda + a)t} \mathscr{L}^{-1}\{\bar{C}(0, s) \, e^{af(s)t}\}, \tag{4}$$

where

$$f(s) = \int_0^\infty e^{-sx} \frac{dP(x)}{dx} dx \quad \text{and} \quad \bar{C}(0, s) = \int_0^\infty e^{-sl} C(0, l) \, dl$$

and the symbol $\mathscr{L}^{-1}$ stands for the inverse of the Laplace transform.

Using (1), we can write

$$N_{T, l} = e^{-(\lambda + a)(T - T_0)} \mathscr{L}^{-1}\{\bar{C}(0, s) \, e^{af(s)(T - T_0)}\} \quad \text{for } T > T_0,$$

and defining

$$\bar{N}_{0, s} = e^{(\lambda + a)T_0} \bar{C}(0, s) \, e^{-af(s)T_0}, \tag{5}$$

we arrive at

$$N_{T, l} = e^{-(\lambda + a)T} \mathscr{L}^{-1}\{\bar{N}_{0, s} \, e^{af(s)T}\} \quad \text{for } T > T_0. \tag{6}$$

In the above equation $N_{T, l}$ is defined only for $T > T_0$. *We now redefine $N_{T, l}$ by dropping this restriction.* Of course, $N_{T, l} \, dl \, dT$ for $T < T_0$, as calculated by (6), is *not* equal to the number of snails whose age is between T and $T + dT$ living between l and $l + dl$. In fact, for ages less than T_0, we do not know what the age distribution is because λ depends strongly on T in this region. Now, let $N^*_{T, l} \, dl \, dT$ be the number of snails whose age is between T and $T + dT$ living between l and $l + dl$. Of course, $N^*_{0, l} \, dl$ is numerically equal to the number of snails born per unit of time between l and $l + dl$. Let $F(T, l)$ be a function such that $F(0, l) = 1$ for all l, and $F(T, l) \sim 0$ for $T > T_0$, that is, very small for $T > T_0$. We can therefore write for all ages

$$N^*_{T, l} = N_{T, l} + (N^*_{0, l} - N_{0, l})F(T, l), \tag{7}$$

where, of course,

$$N_{0, l} = \mathscr{L}^{-1}\{\bar{N}_{0, s}\}. \tag{8}$$

The interpretation of $N_{0, l}$, and hence that of $\bar{N}_{0, s}$, follows immediately from (6). $N_{0, l} \, dl \, dT$ is the number of snails among the $N^*_{0, l} \, dl \, dT$ which will evolve in time according to (3), and a substantial part of them will reach ages older than

T_0.   All the other $(N_{0,l}^* - N_{0,l})$ will be eliminated before T_0, in the process of population control.

Let us now examine the behavior of $N_{T,l}$ when $l \to 0$ and when $l \to \infty$. This can be done without explicit knowledge of $f(s)$ in (7).   We shall use the initial and final limit theorems of the inverse transform (Doetsch, 1961).

Defining

$$\bar{N}_{T,s} = \mathscr{L}\{N_{T,l}\}, \tag{9}$$

it follows from (6) that

$$\bar{N}_{T,s} = \bar{N}_{0,s}\, e^{-(\lambda+a)T+af(s)T}. \tag{10}$$

Hence, since $\lim_{s \to \infty} f(s) = 0$, we have

$$\lim_{s \to \infty} s\bar{N}_{T,s} = e^{-(\lambda+a)T} \lim_{s \to \infty} s\bar{N}_{0,s}\, e^{(a)f(s)T}$$

$$= e^{-(\lambda+a)T} \lim_{s \to \infty} s\bar{N}_{0,s}. \tag{11}$$

Therefore, applying the initial limit theorem we have

$$N_{T,0} = \lim_{l \to 0} N_{T,l} = e^{-(\lambda+a)T} \lim_{s \to \infty} s\bar{N}_{0,s}$$

$$= e^{-(\lambda+a)T} \lim_{l \to 0} N_{0,l} = N_{0,0}\, e^{-(\lambda+a)T}. \tag{12}$$

Similarly, since $\lim_{s \to 0} f(s) = 1$, we have

$$\lim_{s \to 0} s\bar{N}_{T,s} = e^{-(\lambda+a)T} \lim_{s \to 0} s\bar{N}_{0,s}\, e^{(a)f(s)T} = e^{-\lambda T} \lim_{s \to 0} s\bar{N}_{0,s}.$$

Applying, now, the final limit theorem, we have

$$N_{T,\infty} = \lim_{l \to \infty} N_{T,l} = e^{-\lambda T} \lim_{s \to 0} s\bar{N}_{0,s} = N_{0,\infty}\, e^{-\lambda T}. \tag{13}$$

Let us now define the quantity

$$\alpha(T, l) = \frac{\int_T^\infty N_{T,l}\, dl\, dT}{\int_{T_1}^\infty N_{T,l}\, dl\, dT} \quad (T > T_1 > T_0),$$

which is the probability of snails older than T be found in a sample picked between l and $l + dl$, and where all the snails are older than T_1.

From (12) and (13), we have

$$\alpha(T, 0) = \frac{e^{-(\lambda+a)T}}{e^{-(\lambda+a)T_1}} = e^{-(\lambda+a)(T-T_1)}, \tag{14}$$

$$\alpha(T, \infty) = \frac{e^{-\lambda T}}{e^{-\lambda T_1}} = e^{-\lambda(T-T_1)}. \tag{15}$$

Then let α_c be a value of $\alpha(T, l)$, which at one extreme is so small that it will virtually be impossible to find snails whose age is greater than the associated age $T_c(l)$. This age T_c will be taken as the maximum one reached between l and $l + dl$.

From (14) and (15), it follows that

$$T_c(0) = \frac{-\log \alpha_c}{(\lambda + a)} + T_1, \tag{16}$$

$$T_c(\infty) = \frac{-\log \alpha_c}{\lambda} + T_1. \tag{17}$$

Equations (16) and (17) must be compared with the first equation on page 557 of (I). These equations are of the same nature, differing only by the unimportant constant T_1 which, in practice, is small compared with T_c. This points immediately to the conclusion *that the maximum diameter of the snails shell increases progressively from those picked near the spring to those picked near the mouth of the channel.* We owe the knowledge of this phenomenon to a personal communication from Dr. Dobrovolny, who observed its occurrence in swift-flowing creeks. Following his indications, we were able to observe personally its occurrence in Olinda, Pernambuco, Brazil, in a channel draining the spring Bica de S. Pedro, measuring 200 meters from the origin to the outlet in a drain bordering a roadway. The trematodic infection of the snails averaged 1% along the channel and the D_{max} increased gradually from 6 mm. in the spring to 15 mm. at the outlet. This situation remained unchanged until some urbanizing work substituted underground drains for the former open channel. Subsequently, we have recognized, in a qualitative way, the occurrence of the phenomenon in several sites elsewhere.

We would like to point out that the λ appearing in (1) in (I) and (16) and (17) in this paper are not easily measurable. What is easily measurable is the fraction of the population which are infected by trematodic parasites, the quantity we have called p in (I). The relationship between λ and p is one of direct proportionality and have been written in (6) in (I). However, it was pointed out to us by Professor Herbert Landahl that relation (6) in (I) is not general enough. We should have written $\lambda = \beta p + \gamma$ where β and γ are parameters that depend on the fraction of infection by other diseases. This modification, however, does not alter in any way the conclusions of (I). In this paper, λ is also related to p (assumed constant along the channel) by a linear relationship. Since we shall not use this relationship, we shall not pursue this subject any further.

Let us now return to the distribution given by (7), which represents the population aged between T and $T + dT$ living between l and $l + dl$. The $N_{T,l}$ in

(7) is a function of $\bar{N}_{0,s}$, which has little physical significance.   In the remaining part of this paper, it is shown how to express $N_{T,l}$ in terms of the biomass per unit length of the channel.

Employing the notation used in (I, equation 10), and using the same arguments described there, we equate the total food consumed by $N_{T,l}\,dl$ (first part of the population in (7)) per unit time to the total food produced between l and dl in the channel:

$$M(l)\,dl = \frac{A(l)\,dl}{k_1} = \int_0^\infty m(T)N_{T,l}\,dl\,dT, \tag{18}$$

where k_1 is a consumption rate per unit mass of organisms.   The food consumed by the part of the population $(N_{0,l}^* - N_{0,l})F(T,l)$ has been neglected because, as explained in (I), this is small. $M(l)\,dl$ is numerically the mass of organisms which can live between the points l and $l + dl$ of the channel, characterized by the parameters $A(l)\,dl$, which is the quantity of food produced per unit of time between l and $l + dl$.

Taking the Laplace of (18), and using (10), we find

$$\bar{M}(s) = \int_0^\infty m(T)\bar{N}_{0,s}\,e^{-(\lambda+a)T}\,e^{(a)f(s)T}\,dT; \tag{19}$$

and since $\bar{N}_{0,s}$ is independent of T, we can take it outside the integral and write it as

$$\bar{N}_{0,s} = \frac{\bar{M}(s)}{\int_0^\infty m(T)\,e^{-(\lambda+a)T}\,e^{(a)f(s)T}\,dT} \tag{20}$$

By substituting (20) in (7), we finally arrive at

$$N_{T,l}^* = \mathscr{L}^{-1}\left\{\frac{\bar{M}(s)\,e^{[-\lambda-a+af(s)]T}}{\int_0^\infty m(T)\,e^{[-\lambda-a+af(s)]T}\,dT}\right\} + (N_{0,l}^* - N_{0,l})F(T,l). \tag{21}$$

Equation (21) shows that the population in the channel is composed of two groups.   One of them $(N_{0,l}^* - N_{0,l})F(T,l)$ consists of very young organisms existing only because of the great excess of births among planorbid snails.

We will consider only the part of the population given by the first term in (21). For the sake of avoiding the formal complications involved, we will limit ourselves to the study of conditions in the origin and in the mouth of the channel.

We can simplify further by assuming $M(l) = M$.   In this case $\bar{M}(s) = M/s$. Then, from (19) and using the initial limit theorem, we obtain

$$N_{T,0} = \lim_{l\to 0} N_{T,l} = \frac{M\,e^{-(\lambda+a)T}}{\int_0^\infty m(T)\,e^{-(\lambda+a)T}\,dT}. \tag{22}$$

Similarly,

$$\lim_{s \to 0} s\bar{N}_{T,s} = \frac{M e^{-\lambda T}}{\int_0^\infty m(T) e^{-\lambda T} dT}.$$

Therefore, using the final limit theorem, we get

$$N_{T,\infty} = \lim_{l \to \infty} N_{T,l} = \frac{M e^{-\lambda T}}{\int_0^\infty m(T) e^{-\lambda T} dT}. \qquad (23)$$

It is therefore possible to calculate the whole amount of snails per length unit of the channel, at the spring, that is, in $l = 0$, and also very far from the spring, that is, when $l \to \infty$:

$$\mathscr{N}_{T,0} = \int_0^\infty N_{T,0} \, dT = \frac{M}{(\lambda + a) \int_0^\infty m(T) e^{-(\lambda + a)T} dT} = \frac{M}{\lambda_1 \mathscr{L}_{\lambda_1}\{m(T)\}}, \quad (24)$$

$$\mathscr{N}_{T,\infty} = \int_0^\infty N_{T,\infty} \, dT = \frac{M}{\lambda \int_0^\infty m(T) e^{-D\lambda T} dT} = \frac{M}{\lambda_2 \mathscr{L}_{\lambda_2}\{m(T)\}}, \quad (25)$$

where $\lambda_1 = (\lambda + a)$ and $\lambda_2 = \lambda$.

Equations (24) and (25) must be compared with the second equation on page 561 in (I). From them, *we see that the density of snail population decreases progressively from the channel's spring to its outlet.*

According to what we have said before in this paper, the hypothesis used in the integration of (2) fits better in the case of high, regular and uniform channels or ditches. It is even possible to consider the experimental determination of the form of function $P(\xi)$. Radioactive tagging of the snails (Knight *et al.*, 1968) could possibly be used for this determination. Once $P(\xi)$ is obtained, $N_{T,l}$ can be calculated explicitly by (21). But since the resulting expressions are complicated, they are omitted here.

As we have shown in (I), the saturating equilibrium cannot be reached in the snail populations when the trematodic infection increases beyond a certain value. Experimentally, this means that the snails become extremely scarce every time this occurs. From a practical point of view, this means the possibility of controlling the snail associated bilharzian endemics. The exploitation of this possibility requires a rather good determination of the threshold zone, beyond which the saturating equilibrium can no longer exist, and a fair knowledge of the detailed behavior of the snail population. The use of channels might be a powerful tool to study those aspects of the ecology of the *Biomphalaria glabrata*.

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