A MODEL FOR POPULATIONS REPRODUCING BY FISSION[1]

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Abstract. A partial differential equation which describes the dynamics of a single species population for animals reproducing by fission is set forth. The equation is then applied to *Dugesia tigrina.* Whenever possible, experimental results are used to determine pertinent parameters. Tests are performed to determine those parameters upon which the model has a critical dependence. The model gives results which are qualitatively in agreement with empirical populations.

The objective of this paper is to present a deterministic model describing the dynamics of single species populations of organisms reproducing by binary fission. These organisms seem well suited for such studies because of their relative simplicity. Frequently the important physiological characteristics of these organisms can be described by their size alone. The model allows the two parts resulting from fission to be of differing sizes and allows for a delay in the development of one part. We begin by formulating a basic model of the population dynamics in the form of a partial differential equation. The model is then applied to populations of the planarian worm *Dugesia tigrina.* The functions appearing in the equation are constructed from existing experimental data. It should be noted that frequently these data are inadequate for our purposes and so many assumptions are made. The equation containing the assumed functions for *Dugesia* is referred to as the "standard model" and solutions to the equation are obtained. Next we examine the sensitivity of the standard model to the assumptions made and thus determine those factors which most strongly affect the predictions of the model.

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THE BASIC MODEL

First consider the case of simple fission in which organisms divide into two identical parts, each having one-half the mass of the parent. It is assumed that only the mass of the organism affects the birth rate and other important physiological characteristics. This allows us to consider the physiological properties of an organism in a specified environment as being determined by mass only.

We introduce the density function $\rho(t,m)$. The

total number of organisms between the masses (m_1,m_2) at time t is given by

$$\int_{m_1}^{m_2} \rho(t,m)\,dm. \qquad (1)$$

If m_1 is chosen to be zero and m_2 infinity, the integral (1) yields the total number of organisms in the population. We must also define a function $b(t,m)$, the rate at which an organism of mass m at time t divides. The mass density function $\rho(t,m)$ satisfies the partial differential equation

$$\frac{\partial \rho(t,m)}{\partial t} + \frac{\partial [g(t,m)\,\rho(t,m)]}{\partial m}$$
$$= -b(t,m)\,\rho(t,m) + 2[2b(t,2m)\,\rho(t,2m)] \qquad (2)$$

where the function $g(t,m)$ is the average rate of growth for an organism of mass m at time t.

Equation (2) is a continuity equation. Continuous changes in organism mass are accounted for by the left-hand side of the equation. The reproduction process is described by the right-hand side where the first term accounts for individuals of mass m which give birth and fall to a lower mass. The last term accounts for organisms of mass $2m$ dividing into two individuals of mass m. The "2" outside the brackets corresponds to the two individuals the parent becomes and the "2" inside the brackets arises from the fact that animals falling into the interval $(m, m + \Delta m)$ come from the larger interval $(2m, 2m + 2\Delta m)$.

In many cases, e.g., planarians, the process of fission is more complex. Here the original animal breaks into a parent animal and an offspring. If the mass of the offspring is denoted by $H \cdot m$ just after fission, then the parent retains a mass of $(1 - H) \cdot m$. When the offspring requires some time after fission to develop into an individual capable of growth we denote the time required for this process by τ. After the time interval τ the offspring is referred to as a neonate and its mass is given by hHm, where h is the fraction of mass retained after τ. The mass density function $\rho(t,m)$ satisfies the partial differential equation

$$\frac{\partial \rho(t,m)}{\partial t} + \frac{\partial [g'(t,m)\,\rho(t,m)]}{\partial m}$$

$$= -b(t,m)\,\rho(t,m) +$$

$$\frac{1}{1-H}\,b[t,m/(1-H)]\,\rho[t,m/(1-H)] +$$

$$\frac{1}{hH}\,b[t-\tau,m/(hH)]\,\rho[t-\tau,m/(hH)]\,. \quad (3)$$

As in equation (2), continuous changes in mass are accounted for by the left hand side of this continuity equation. The first term on the right hand side accounts for animals of mass m which give birth and fall to a lower mass, the second term for animals of higher mass which give birth and fall to mass m, and the last term accounts for the number of neonates (offspring which have just developed into viable individuals) of mass m. A formal derivation is given in Sinko (1969).

The equation can be generalized to cases in which age affects important physiological characteristics or where the organisms are subject to death (see Sinko 1969).

To apply the model we construct the functions g and b, specify the initial number of animals and their masses, and estimate H, h, and τ.

Applying the Model to *Dugesia*

In the experimental *Dugesia tigrina* populations considered here (Armstrong 1959, 1964) reproduction was entirely by the asexual process of binary fission, the tail of a worm breaking away from the parent and developing into a new worm. The animals were kept in 120 ml of conditioned tap water in finger bowls. Every second day for a total 102-day period each population of flatworms was allowed to feed for 3 hours on 0.1 ml of freshly hatched and killed brine shrimp. After feeding the animals were censused and placed in fresh water.

Deaths among feeding individuals were negligible, and those that occurred were caused by isolated accidents. No signs of "senescence" were observed in any of the populations, and for all practical purposes, feeding individuals in these populations can be regarded as immortal. The only mortality resulted from cannibalism of undeveloped tails by feeding individuals.

In Armstrong's populations designated 1–1, 1–2, and 1–3 an increased reproduction rate was simulated by adding tails for each tail produced by members of the population. Only the population designated 1–0, to which no tails were added, is considered here because the methods used for estimating the number of tails in the other populations were inconsistent (see Sinko 1969).

As far as can be determined from the available

data, only the mass and not the age of a feeding individual affects its birth rate or any other important physiological characteristic. This combined with the absence of death and senescence in feeding individuals allows us to consider the physiological properties of an animal as determined by its mass only. A new tail of course does not behave like a feeding individual, but this is taken into account by using a time lag in the births of new animals so that tails are regarded as being born when they start feeding. The time lag, τ, is the length of time it takes for a tail to develop into a feeding individual.

Initial mass distribution, $\rho(0,m)$

Armstrong's populations begin with 9 adults and 26 small animals. All but three small and one adult animal(s) have tails. He considers the minimum adult length to be "about 17 mm," which for his population 1–0' (under equilibrium conditions) corresponds to 0.76 mg. We take 0.7 mg for the minimum adult mass and assume that the initial mass distribution is Gaussian (normal) with mean 0.5695 mg and standard deviation 0.2 mg,

$$\rho(0,m) = \frac{175}{(2\pi)^{1/2}}\,e^{-12.5(m-0.5695)^2}$$

when $0.05\text{ mg} \leq m \leq 1.2\text{ mg}$

$$\rho(0,m) = 0$$

when $m < 0.05\text{ mg}$, or $m > 1.2\text{ mg}$.

This distribution corresponds to 26 animals with $m < 0.7$ mg and 9 animals with $m > 0.7$ and nearly all of the distribution falls in the size range of the animals Armstrong investigated.

Growth function, $g(t,m)$

The growth function is proportional to the difference between food intake and food required for maintenance. The latter depends on the maintenance efficiency, E_m, which we define as the ratio of the dry mass of food consumed during a 2-day feeding interval to the dry mass of the animals when the population is in equilibrium. This definition is the inverse of that given by Armstrong. Armstrong found that the amount of food required for maintenance is (approximately) directly proportional to the mass of the animal, i.e., E_m is constant and equal to 0.141 for his population 1–0.

Since little or no data relating to food intake as a function of mass exists for *Dugesia*, we assume that small animals receive more food per unit mass than do large animals. This is in agreement with the data obtained by Richman (1958) for *Daphnia*. More precisely, we assume the food intake in-

creases as the square root of the mass in the standard model,

$$\text{Food intake} = \frac{\sqrt{m}\,\mathbf{F}}{C} \,,$$

where $\mathbf{F}$ is the total food eaten by the population in each feeding period and C is a normalization constant given by

$$C = \int_0^\infty \sqrt{m}\,\rho(t,m)\,dm \,,$$

so that the total food intake is $\mathbf{F}$. Note that as the population density ρ changes with t, C also varies. We take $\mathbf{F} = 5.2$ mg according to Armstrong (1959).

Subtracting the food required for maintenance from food intake gives the amount of food an animal has available for growth. This must be multiplied by an assimilation efficiency, E_a, defined as

$$E_a = \frac{\text{New animal mass}}{\text{Mass of food available for growth}} \,,$$

to give the growth function

$$g_s(t,m) = E_a \left[\frac{\sqrt{m}\,\mathbf{F}}{\int_0^\infty \sqrt{m'}\rho(t,m')\,dm'} - E_m m \right] \,,$$

where m' is a variable of integration. Since values of E_a are not available we assume $E_a = 0.45$ for the standard model. A minimum estimate of E_a is 0.25 (see Sinko 1969).

The behavior of g_s (and other growth functions) as a function of m is shown in Figure 1. At $t = 0$ there is a sufficient supply of food and all animals grow. At a later time the normalization constant C has increased, since the population increased. Thus the relative food supply is lower and only animals less than 0.45 mg grow; larger animals decrease in mass. Consequently, the population tends toward a uniform mass after births cease.

Birth function, $b(t,m)$

The birth function describes the number of tails produced. Armstrong found that well-fed worms produced a tail every 8 days and that food shortages end the production of tails. Since no further appropriate experimental data exists we assume a birth function b_1 in our standard model. This function, illustrated in Figure 2, assigns a probability of producing a tail within a 2-day period, which is a function of mass. It assumes that a large worm is more likely to produce a tail than a smaller one and in particular worms of 1 mg mass have probability 0.25, which equals the maximum rate (one tail in 8 days) Armstrong found. A probability 1 is assigned to very large animals and those with mass less than 0.5 mg cannot reproduce. Furthermore, if an animal of any mass receives less food than required for maintenance its birth rate is set equal to zero.

Paramters H, h, and τ

The data in Figure 2 of Armstrong (1964) illustrate the relation between the length of a new tail and the length of the parent before separation, which is approximately constant and equal to 0.3. It will be assumed here that the mass of the tail
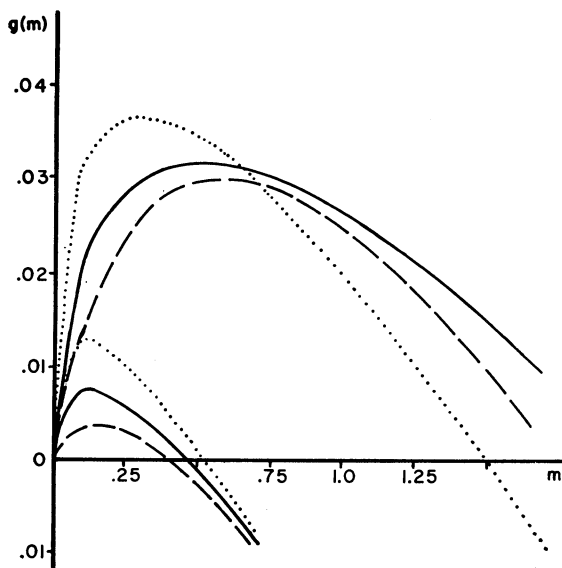

FIG. 1. The solid lines represent the square root growth function used in the standard model. The upper lines are at time zero, the lower lines at time 100 days. The cube root and logarithmic growth functions are represented by the dotted and dashed lines respectively.
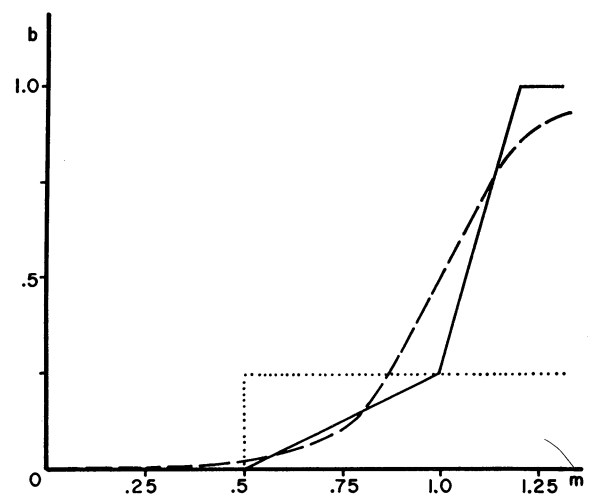

FIG. 2. The birth function used in the standard model, b_1, is represented by the solid line. The dashed line is birth function b_2 and the dotted line is b_5.

is $H \cdot m$ where m is the original mass of the parent, and the mass of the parent becomes $(1 - H) \cdot m$ after the tail breaks off. Although this assumption seems reasonable we note that Armstrong (1959) states that "the data are inadequate to yield a length-weight relationship." The value of H is taken as 0.2 in the standard model. No data exists for determining the fraction of original mass retained by the tail during the time it develops into a feeding individual. It is taken as $h = 0.9$ in the standard model.

The average time required for a tail to develop into a feeding individual, τ, is found by integrating the graphs given by Armstrong (1964) to find the total number of tails times the time it took each tail to develop. When this number is divided by the number of new individuals we find $\tau = 6.6$ days for population 1–0 and from 5.3 to 7.0 days for the other populations. In the standard model $\tau = 6$ days.

Solution of the standard model

To solve equation (3) we used a method of integrating along the characteristics (see Fox 1962, Sinko 1969).

Figure 3 compares the results of the calculations based on the standard model with Armstrong's experimental population. The agreement is quite good, but the experimental populations exhibit some irregularities not present in the calculations. These irregularities may occur because of the small size of the population. If, for example, most of the animals produce tails almost immediately few tails would be produced during the next 8 days. Environmental influences may also be responsible. All of Armstrong's populations show a synchronous rise in births at $t = 54$ days which may have been caused by temperature variation. Armstrong did not have available a constant temperature cabinet during the first 76 days and the temper-

ature varied by more than 10°C. Kenk (1937) found that a change of this magnitude has a very noticeable effect on the reproductive rate of *D. tigrina*.

Testing the model for critical dependence

Since it was necessary to make many assumptions to construct the model it is important to determine which factors most strongly affect the results.

We find that large changes in the initial mass distribution have only slight effects on the population growth curves and therefore a precise knowledge of the initial distribution is not needed.

Varying the assimilation efficiency, too, does not greatly affect the population. Values of E_a between 0.15 and 0.90 result in final populations which differ by only 12%. Higher values of E_a lead to slightly higher biomass, more rapid initial population increase, and shorter elapsed time before equilibrium. For $E_a = 0.75$, the elapsed time was 52 days, while for $E_a = 0.25$, it was 94 days.

Various growth functions were also used. Instead of assuming the amount of food an animal receives is proportional to the square root of its mass, new functions g_c and g_l, with a cube root and logarithmic dependence were studied, viz.,

$$g_c(t,m) = E_a \left[\frac{\mathbf{F} \sqrt[3]{m}}{\int_0^\infty \sqrt[3]{m'} \, \rho(t,m') \, dm'} - E_m m \right],$$

$$g_l(t,m) = E_a \left[\frac{\mathbf{F} \log_e (5m + 1)}{\int_0^\infty \log_e (5m' + 1) \, \rho(t,m') \, dm'} - E_m m \right],$$

where m' is a variable of integration. Graphs of these functions, and of g_s used in the standard model appear in Figure 1. The figure shows the various g functions for population 1–0 both at time zero and at time 100 days. The values of the constants are $E_a = 0.45$, $\mathbf{F} = 5.2$ mg, and $E_m = 0.1415$, the values used in the standard model.

The cube root g_c function yields a higher growth rate for small animals and a lower one for large animals than does the square root g_s function. As expected, g_c leads to a model population in which animals are more uniform in size than those in the standard model. The use of g_c also resulted in the equilibrium number of animals being 8% lower; presumably because some of the food which was consumed by larger animals (and hence used primarily for reproduction) in the standard model was consumed by smaller animals who used the food to increase their own size.

As shown in Figure 1, the function g_l gives growth rates which are slightly lower than those
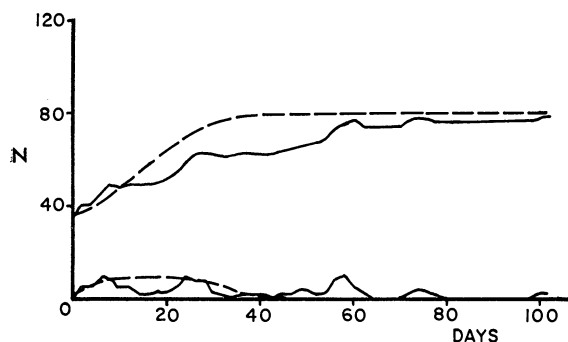

FIG. 3. The history of Armstrong's population 1–0 (solid lines) and the standard model for population 1–0 (dashed lines). The upper lines represent the total numbers of animals and the lower lines represent the numbers of tails.

for g_s at time zero, and considerably lower at time 100. The equilibrium level of the model population regulated by g_l was 10% higher than that of the standard model, presumably because the lower growth rates retard the growth of small animals and allow most of the food to go to larger animals who use it to produce more tails. The g_l function resulted in a higher portion of small animals.

A number of different birth functions were also studied. In the standard model an animal must receive more food than needed for maintenance before it can produce a tail [i.e., $g(t,m) \geqq 0$]. A model was examined in which an animal was required to grow at least 0.005 mg during a 2-day period before it could produce a tail [i.e., $g(t,m) \geqq 0.005$]. Tail production stopped much sooner.

The birth function $b_2(t,m)$, illustrated in Figure 2, allows worms of all sizes to reproduce provided they receive more food than is required for maintenance [$g(t,m) \geqq 0$]. In the model population regulated by $b_2(t,m)$, tail production did not completely stop after 100 days although it was at a very low level after 62 days, the equilibrium time for the standard model.

Birth function b_3 is the same as b_2 except that animals of mass less than 0.5 mg cannot reproduce (the same is true for the birth function used in the standard model). The model population regulated by b_3 has a history that is almost identical to that of the standard model. This history is more realistic than b_2 because of the complete cessation of tail production. Apparently the minimum size at which an animal can reproduce strongly influences the growth characteristics of the population. To further test this, birth function b_4, similar to the standard birth function except that animals as small as 0.4 mg can reproduce, was examined. The population governed by b_4 reached equilibrium later than the standard population.

The effects of much higher birth rates for relatively small animals are illustrated by birth function b_5. In this birth function all animals of mass 0.5 mg or greater having a growth rate of at least 0.005 mg per 2-day period are assumed to have a 25% chance of producing a tail in a 2-day period, while all other worms have no chance of producing a tail. The production of tails is much higher during the first 15 days in the model population regulated by b_5 than it is in the standard model and the equilibrium level is reached sooner and is 20% higher.

Cannibalism

We postulate a very simple law governing cannibalism: tails have a probability P of being eaten within the first 2 days after separation. This probability is no doubt strongly dependent on food

supply, and to a lesser extent on the numbers of tails and feeding animals. In performing the calculations the masses of tails consumed must also be added to the food supply. With $P = 0.3$ and the mass of an individual tail $m_T = 0.13$ mg the total mass of tails eaten is 19.2 mg compared to 260 mg of total food. The model population which results resembles the experimental population 1–0 more closely than does the standard model (see Fig. 4).
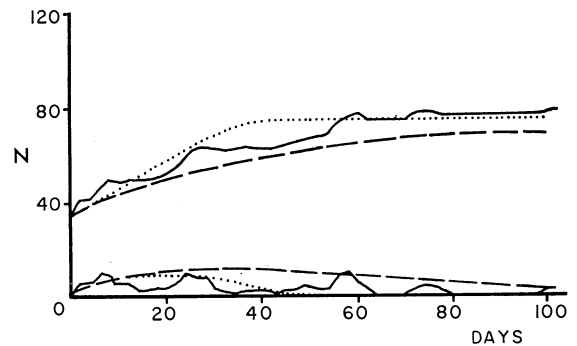

FIG. 4. Armstrong's experimental population 1–0 (———), and the model incorporating cannibalism with $P = 0.3$ (······) and $P = 0.78$ (------). The lower lines represent the numbers of tails.

Larger values of P lead to smaller rates of growth for the total population and consequently delayed equilibrium. For example, with $P = 0.78$ (as estimated by Armstrong), the model population requires 100 days to reach equilibrium. This may occur because either Armstrong's estimate of P is in error or the mathematical model is inaccurate. We believe the former is the case since Armstrong's estimate is based on observations of postpharyngeal scars in food-limited populations and calculations from life table studies of amply fed populations. It is possible that scars heal much more rapidly in the amply fed populations than in population 1–0. This would account for the large overestimate in P.

CONCLUSIONS

The application of our model to *Dugesia,* in this paper, involved more assumptions than our previous work on *Daphnia* (see Sinko and Streifer 1969), because of the relative lack of appropriate experimental data relevant to *Dugesia.* Consequently, the effects of varying the birth and growth functions were studied more extensively. It seems likely that the square-root growth function g_s and a birth function such as b_1 or b_3 which limit births to animals greater than 0.5 mg are the most realistic of those examined. However, since the effects of cannibalism are inadequately understood, the model cannot be completely verified. The model

could be checked by experimentally studying *Dugesia* which do not practice cannibalism.

It should also be noted that length rather than mass could be used as a describing characteristic of the animals, but no simplification would result.

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