

AN ABSTRACT OF THE THESIS OF

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Title: MOVEMENT OF POPULATION IN RESTRICTED REGIONS

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Mathematicians have been concerned with population growth and movement since the days of Leonhard Euler and Thomas Malthus. Chapter I of this paper sketches the history of the development of the modern population theory.

In Chapter II, a partial differential equation is derived which governs the growth and movement of populations in definite regions. This general fundamental equation lends itself to many applications including: roaming nomads; bacteria growth, urban growth; one specie preying upon another; and finally I have used the equation to model spawning salmon.

Movement of Populations in
Restricted Regions

by

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
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
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MOVEMENT OF POPULATIONS IN RESTRICTED REGIONS

I. HISTORICAL INTRODUCTION

Thomas Malthus (1766-1834), in his three volume: Essay on the Principles of Population, 1798, coined the fundamental idea that population, when unchecked, grows exponentially. In Malthus' own words, "It goes on doubling itself at regular intervals, or increases in a geometrical ratio." Malthus noted in Volume I of his work that in the town of Berne, out of 487 notable families, 379 became extinct in the span of two centuries, from 1583 to 1783. That is, while the population as a whole showed rapid growth, individual family lines tended to extinction. The theory of branching processes may be said to have had its birth from the realization that such paradoxes are not just the result of some extraordinary circumstances.

The French statistician L. F. Benoiston de Chateauneuf (1776-1856) had studied noble families founded in the tenth to the twelfth centuries and estimated their duration to be three hundred years. Another Frenchman, I. J. Bienaymé (1796-1878) treated the problem mathematically and seems to have been able to determine the correct relationship between the probability of a family's extinction and the mean number of male children per father.

The real credit for the formulation of the problem belongs to Sir Francis Galton (1822-1911), a cousin of the famous Charles Darwin, who studied the decline of English nobility. Galton stated the problem of the extinction of families in the "Educational Times," 1873, as follows:

Problem 4001: A large nation, of whom we will concern ourselves with the adult males, N in number, and who each bear separate surnames, colonize a district. Their law of population is such that in each generation, a_0 per cent of the adult males have no male children who reach adult life; a_1 have one such male child; a_2 have two; and so on up to a_5 who have five. Find (1) what proportion of the surnames will have become extinct after r generations; and (2) how many instances there will be of the same surname being held by n persons.

When Galton received no adequate answers to his publication he sought out his friend, the clergyman and mathematician Rev. H. W. Watson. Because of an algebraic oversight Watson failed to solve the problem entirely correctly. He managed, however, to transform the problem into one of iteration of generating functions similar to the way it is still treated today. The mathematical model formulated by Galton and Watson has become appropriately known as the Galton-Watson branching process.

The problem remained dormant for half a century until 1922 when R. A. Fisher introduced Galton's problem into population genetics and the survival of mutant genes. Five years later, J. B. S. Haldane (1892-1964), the biochemist, psychologist, geneticist,

biomathematician, and political publicist again applied the model to genetics and solved Fisher's problem.

The first complete and correct determination of the extinction probability for the Galton-Watson process was submitted by J. F. Steffensen, a Danish actuary, in 1930. The problem was also handled by the Russian A. N. Kolmogorov who, in 1938, determined the asymptotic form of the probability that a family will still exist after a very large finite number of generations.

While in general, populations are much more complex than the problem of Galton, in the beginning

branching processes were thus tightly interwoven with demographic considerations. The main stream of demography, however, for obvious reasons, was less concerned with family extinction than with properties of entire populations, like growth and composition. The founders of modern demography were empirical scientists. They measured frequencies of birth and death, evaluated ratios of births to marriages, and constructed the first life tables [1, p. 3].

The idea was to search out consistencies in order to predict future population.

One of these demographers was the clergyman Johann Peter Süßmilch (1707-1767) who was of the opinion that the universe was divinely ordered in a mathematical sense. Süßmilch, a friend of Leonhard Euler, on occasion sought the help of the famous mathematician. It was thus that Euler came to lay the groundwork for what is today known as the "stable population theory." Euler formulated

the principle of exponential growth in his Introductio in analysin infinitorum (1748) and concluded that:

For that reason are the objections of these incredulous men, who deny that in such a short space of time the whole earth could have been filled with inhabitants descending from one man, utterly ridiculous.

Euler treated homogeneous asexually reproducing populations and showed that a

hypothetical closed population with a given time invariant age specific mortality and fertility and a constant rate of (i. e. exponential) increase must have a fixed age distribution [1, p. 4].

He was thus concerned with the relationship between age structure and fertility-mortality.

Euler's work in this field also was neglected for more than half a century until 1839 when it was again taken up by Ludwig Moser Königsberg who applied it to his studies of the populations of the United States and France. After Königsberg, the door seems to have been opened and many men followed suit in taking up the idea. Such men as the great Belgian statistician Adolphe Quételet (1796-1874) and the important work of the two actuaries Alfred Lotka (1880-1949) and L. Herbelot who share credit for the modern stable population theory were some of the more important of these men.

Thus, it came to be that in the early twentieth century there were two schools of thought concerning problems of population development. One was the Galton-Watson branching process, which

considered the fate of individual family lines in a growing population and was of a probabilistic nature. The other was the Euler-Lotka stable population theory.

Slowly but surely, as more and more complex branching models were considered, the two views came together. The coalescence of the two theories was brought about by many great names of modern mathematics.

Some of these men were George Yule (1871-1951), W. H. Furry (1907-) and William Feller (1906-1970) working with "continuous time processes of a birth-and-death type" [1, p. 5]. And so it was about this time (1926) that Vito Volterra (1860-1940), then professor at the University of Rome, began his investigation of competing species. Volterra's work is of particular importance to the writing of this paper and thus deserves more careful consideration.

Volterra's friend U. D'Ancona had made a statistical analysis of the fish being caught in the Adriatic Sea. Evidently, there was a periodic flux between plentiful food fish followed by an increase in predators such as sharks and rays which in turn brought a decline to the food fish population, then a decline in predators due to lack of food so that again the food fish flourished, and so on.

This phenomenon was described by Volterra's pair of differential equations [5, p. 7]:

$$\frac{dN_1}{dt} = \alpha_1 N_1 - \lambda_1 N_1 N_2$$

$$\frac{dN_2}{dt} = -\alpha_2 N_2 + \lambda_2 N_1 N_2$$

where α_i and λ_i are positive constants so that $-\lambda_1 N_1 N_2$ gives the loss rate of small fish (prey) due to "collisions" with larger ones (predators), and $\lambda_2 N_1 N_2$ gives the growth rate of the larger fish as a result of the same collisions. Here species 1 would describe the usual Malthusian exponential growth in the absence of species 2, while species 2 would die out in the absence of species 1.

The work of these men and their continuous time processes was brought to a head and summed up by David Kendall in his book, Stochastic Processes and Population Growth (1949).

On the other hand, the Galton-Walton process was being generalized by such investigators as Richard Bellman and Theodore Harris.

After 1940, interest in the model increased, partly because of the analogy between the growth of families and nuclear chain reactions, and partly because of the increased general interest in applications of probability theory [4, p. 2].

In 1963, Harris's book, The Theory of Branching Processes, summed up the whole train of thought and laid the basis for further research and more rapid progress.

Introductory Summary of Thesis

The usual formulation of the equations governing the growth of populations leads to a system of ordinary differential equations for the total population of the specie or species in question. Consequently, the predictions are global, if natural and local variations in the populations are neglected. The purpose of this paper is to derive a partial differential equation governing the population density and then to apply the results to a few simple examples.

II. DERIVATION OF PARTIAL DIFFERENTIAL EQUATION

We shall be working in two dimensional Euclidean space, R^2 . Points in R^2 are denoted by (x, y) , (ξ, η) , etc; t, τ will denote time variables. Let $u = u(x, y, t)$ denote the population density in (x, y) at the time t . That is, if A is any region in R^2 with a smooth boundary (i. e., if the boundary of A is parameterized by $(\xi(s), \eta(s))$ where $\xi(s)$ and $\eta(s)$ are twice continuously differentiable functions) then

$$N_A(t) = \iint_A u(x, y, t) dx dy$$

gives the number of individuals, N_A , in A at the time t . The change per unit of time in $N_A(t)$ is

$$(1.1) \quad N'_A(t) = \iint_A u_t(x, y, t) dx dy$$

Now let B denote the boundary of A , ν the unit exterior normal to B , ds an element of length on B , $\bar{q}(x, y, t)$ the number of individuals passing over an arc, ds , per unit time, so that $-\int_B \bar{q} \cdot \nu ds$ gives the net emigration from A . Finally, let $\phi(x, y, t)$ give the number of births per unit area and $\psi(x, y, t)$ the number of deaths per unit area. Then, the change per unit time in $N_A(t)$ can

be represented as

$$(1.2) \quad N'_A(t) = - \int_B \bar{q} \cdot \nu ds + \int_A \varphi dx dy - \int_A \psi dx dy$$

To obtain a mathematically tractable problem, it is necessary to have reasonable expressions for \bar{q} , φ , and ψ in terms of u , x , y , and t .

Consider first \bar{q} . We shall assume that, unless there are other effects present, the natural tendency is to move from areas of high population concentrations to areas of lower concentrations. At the same time, due to external conditions (for example: economic in the case of humans, a moving environment such as a stream for bacteria, etc.) there is often a tendency for a population to congregate in certain more attractive areas. Thus, we assume that \bar{q} is of the form:

$$(1.3) \quad \bar{q} = -\alpha \nabla u + u \bar{v}$$

where the vector \bar{v} is an underlying velocity of movement of individuals from one region to another and $\alpha \geq 0$.

Combining (1.1), (1.2) and (1.3) now yields:

$$(1.4) \quad \iint_A u_t dx dy = \int_B (\alpha \nabla u \cdot \nu - u \bar{v} \cdot \nu) ds + \iint_A (\varphi - \psi) dx dy$$

In equation (1.4), the integral:

$$\int_B (\alpha \nabla u \cdot \nu - u \bar{\nu} \cdot \nu) ds = \int_B (\alpha \nabla u - u \bar{\nu}) \cdot \nu ds$$

We have assumed that B is a sufficiently smooth closed curve and that u is continuous and has continuous first and second order partial derivatives on A . Thus, applying the Gauss divergence theorem (Green's theorem in the plane) we get

$$\int_B (\alpha \nabla u - u \bar{\nu}) \cdot \nu ds = \iint_A \operatorname{div}(\alpha \nabla u - u \bar{\nu}) dx dy$$

Equation (1.4) now becomes

$$(1.5) \quad \iint_A u_t dx dy = \iint_A \operatorname{div}(\alpha \nabla u - u \bar{\nu}) dx dy + \iint_A (\varphi - \psi) dx dy$$

At this point we need the following;

Lemma: If, for every region $A \subset D$ with smooth boundary and continuous $F(x)$, we have

$$\int_A F(x) dx = 0$$

then $F(x) \equiv 0$ in A .

Proof: Suppose $F(x) \neq 0$ on D . Then there exists $\bar{x} = (\bar{x}_1, \bar{x}_2) \in D$ such that $F(\bar{x}) \neq 0$. We may suppose $F(\bar{x}) > 0$. By continuity of F , there exists $\delta > 0$ such that $F(x) > 0$, for all $x \in B(\bar{x}, \delta)$, the ball centered at \bar{x} and radius δ . We now choose $\bar{A} = B(\bar{x}, \delta) \subset D$ to be our region of integration, so that;

$$\int_{\bar{A}} F(x) dx > 0$$

since $F(x) > 0$ on \bar{A} . This is a contradiction since $\int_{\bar{A}} F(x) dx = 0$ for every region $A \subset D$. We conclude $F(x) \equiv 0$.

Invoking the lemma we get our final result, that is;

$$(1.6) \quad u_t(x, y, t) = \text{div}(\alpha \nabla u - u \bar{v}) + (\varphi - \psi)$$

Dimensionally, we have (N is the number of individuals in the population):

$$[u] = N \cdot l^{-2}, \quad [\bar{v}u] = N \cdot l^{-3}, \quad [\bar{v}] = l \cdot t^{-1},$$

$$[\bar{q}] = N \cdot l^{-1} \cdot t^{-1} \quad \text{so that} \quad [\alpha] = l^2 t^{-1}.$$

This coefficient, α , must be determined by experimentation.

At this point in our discussion it is instructive to consider a few simple examples.

III. ROAMING NOMADS

Consider the case of nomads who winter at one place, then move in a fairly straight line to the north, spend the summer and then return to spend the winter. Let us suppose that the population is stable, so that $\varphi - \psi = 0$, and does not spread out, that is, $\alpha = 0$.

Let:

$$\bar{v}(t) = \begin{cases} \bar{v}, & 0 \leq t \leq t_1 \\ 0, & t_1 \leq t \leq t_2 \\ -\bar{v}, & t_2 \leq t \leq t_3 \\ 0, & t_3 \leq t \leq t_4 \end{cases} .$$

Here, t_1 is the time needed to go north; $t_2 - t_1$ is the length of the summer; $t_3 - t_2 = t_1$ is the time needed for the return trip; and $t_4 - t_3$ is the length of the winter. Also, we assume $\bar{v} = (\lambda, \mu)$ is constant.

Let $f(x, y)$ be the initial population density: in this case a function which vanishes identically for (x, y) sufficiently far from (x_0, y_0) , the initial camp-site. Equation (1.6) now becomes:

$$u_t = \operatorname{div}(-u\bar{v}) = -\bar{v} \cdot \nabla u$$

since \bar{v} is a constant vector. The problem to be solved, then, is:

find $u(x, y, t)$ which satisfies the differential equation:

$$(D. E.) \quad u_t = -\lambda u_x - \mu u_y, \quad \text{for all } x, y \in \mathbb{R}, \quad t > 0,$$

subject to the initial condition at $t = 0$

$$(I. C.) \quad u(x, y, 0) = f(x, y).$$

For the solution, we assume $u(x, y, t)$ in the form:

$$u(x, y, t) = f(x+A(t), y+B(t))$$

where

$$A(0) = 0 = B(0).$$

Then

$$u_x = f_x$$

$$u_y = f_y$$

and by the chain rule

$$u_t = A'(t)f_x + B'(t)f_y$$

so that

$$u_t + \lambda u_x + \mu u_y = \lambda f_x + \mu f_y + A'f_x + B'f_y.$$

$$\therefore \quad 0 = [\lambda + A'(t)]f_x + [\mu + B'(t)]f_y$$

Thus

$$A'(t) = -\lambda \quad \text{and} \quad B'(t) = -\mu$$

Integration now yields the functions $A(t)$ and $B(t)$. That is

$$A(t) = A(0) - \int_0^t \lambda dt = - \int_0^t \lambda dt$$

and

$$B(t) = B(0) - \int_0^t \mu dt = - \int_0^t \mu dt$$

Thus, for the solution of the initial value problem we have

$$u(x, y, t) = f(x, y) - \int_0^t \bar{v}(\tau) d\tau .$$

where we are now writing f as a function of a vector. Now we have

$$\int_0^t \bar{v}(\tau) d\tau = (\lambda, \mu)t \quad \text{for } 0 \leq t \leq t_1$$

$$\begin{aligned} \int_0^t \bar{v}(\tau) d\tau &= \int_0^{t_1} \bar{v}(\tau) d\tau + \int_{t_1}^t \bar{v}(\tau) d\tau \\ &= (\lambda, \mu)t_1 \quad \text{for } t_1 \leq t \leq t_2 \end{aligned}$$

$$\begin{aligned} \int_0^t \bar{v}(\tau) d\tau &= \int_0^{t_1} \bar{v}(\tau) d\tau + \int_{t_1}^{t_2} \bar{v}(\tau) d\tau + \int_{t_2}^t \bar{v}(\tau) d\tau \\ &= (\lambda, \mu)t_1 - (\lambda, \mu)\tau \Big|_{t_2}^t \\ &= (\lambda, \mu)t_1 - (\lambda, \mu)[t-t_2] \quad \text{for } t_2 \leq t \leq t_3 \end{aligned}$$

$$\begin{aligned}
\int_0^t \bar{v}(\tau) d\tau &= \int_0^{t_1} \bar{v}(\tau) d\tau + \int_{t_1}^{t_2} \bar{v}(\tau) d\tau + \int_{t_2}^{t_3} \bar{v}(\tau) d\tau + \int_{t_3}^t \bar{v}(\tau) d\tau \\
&= (\lambda, \mu)t_1 - (\lambda, \mu)[t_3 - t_2] \\
&= (\lambda, \mu)t_1 - (\lambda, \mu)t_1 \\
&= 0 \quad \text{for } t_3 \leq t \leq t_4.
\end{aligned}$$

Written out, then, the solution is

$$u(x, y, t) = \begin{cases} f(x - \lambda t, y - \mu t), & 0 \leq t \leq t_1 \\ f(x - \lambda t_1, y - \mu t_1), & t_1 \leq t \leq t_2 \\ f(x - \lambda t_1 + \lambda(t - t_2), y - \mu t_1 + \mu(t - t_2)), & t_2 \leq t \leq t_3 \\ f(x, y), & t_3 \leq t \leq t_4. \end{cases}$$

IV. RADIAL BACTERIA GROWTH

Consider a bacteria culture on a circular dish of radius a . Suppose a very small drop containing N_0 bacteria is initially deposited at the center of the dish. Assume no bacteria can escape through the side of the dish; that the dish is radially symmetric; that the medium is at rest (i. e., $v = 0$) and the rate at which bacteria spread out is $\alpha = 1$. Finally, suppose that $\phi - \psi = \lambda u$.

Equation (1.6) becomes

$$\begin{aligned}
 (3.1) \quad u_t &= \operatorname{div}(\nabla u) + \lambda u \\
 &= \Delta u + \lambda u \\
 &= \frac{1}{r} (ru_r)_r + \lambda u \quad [\text{where we have changed} \\
 &\quad \text{to polar coordinates}]
 \end{aligned}$$

The problem to be solved, then is: find $u(x, y, t)$ satisfying the differential equation;

$$(D. E.) \quad u_t = u_{rr} + \frac{1}{r} u_r + \lambda u, \quad r < a$$

subject to the boundary conditions

$$(B. C.) \quad u \text{ is bounded as } r \rightarrow 0^+$$

$$\frac{\partial u(a, t)}{\partial r} = 0$$

and the initial condition

$$(I. C.) \quad u(r, 0) = N_0 \delta(x, y)$$

where $\delta(x, y)$ is the two dimensional Dirac delta function.

We have: $u_t = \frac{1}{r} (ru_r)_r + \lambda u$ and, letting $u(r, t) = e^{\lambda t} w(r, t)$,

we get:

$$(\lambda w + w_t) e^{\lambda t} = \frac{1}{r} (rw_r)_r e^{\lambda t} + \lambda w e^{\lambda t}.$$

Canceling $e^{\lambda t}$ and subtracting λw from both sides we see that

$w(r, t)$ must satisfy the simpler problem

$$(D. E.) \quad w_t = \frac{1}{r} (rw_r)_r$$

with the boundary conditions

$$(B. C.) \quad \begin{aligned} u_r(a, t) = 0 &\Rightarrow w_r(a, t) = 0 \\ |u(0, t)| < \infty &\Rightarrow |w(0, t)| < \infty \end{aligned}$$

and the initial condition is

$$(I. C.) \quad u(r, 0) = w(r, 0) = N_0 \delta(x, y)$$

To solve, we let

$$w(r, t) = R(r)T(t),$$

then;

$$RT' = \frac{1}{r} (rR')'T$$

$$\frac{T'}{T} = \frac{(1/r)(rR')'}{R} = \mu$$

so that; $T - \mu T = 0$ and $R'' + \frac{1}{r}R' - \mu R = 0$. We now consider the following two cases to determine the eigen values.

Case I. $\mu = \nu^2$, $\nu > 0$, gives rise to the modified Bessel differential equation of order zero

$$R'' + \frac{1}{r}R' - \nu^2 R = 0,$$

which has for its general solution;

$$R = C \cdot I_0(\nu r) + D \cdot (\text{unbounded solution})$$

where C and D are constants. Boundedness implies that $D = 0$ and therefore

$$R(r) = CI_0(\nu r)$$

where

$$I_0(\nu r) = \sum_{\ell=0}^{\infty} \frac{\left(\frac{\nu r}{2}\right)^{2\ell}}{(\ell!)^2}.$$

But,

$$\begin{aligned} R'(r) &= CI_0'(\nu r) \\ &= C \sum_{\ell=1}^{\infty} \frac{\ell \nu \left(\frac{\nu r}{2}\right)^{2\ell-1}}{(\ell!)^2} \end{aligned}$$

which is strictly greater than zero for $r \neq 0$ and $C \neq 0$. Thus,

$$R'(a) = 0 \Rightarrow C = 0 \Rightarrow R(r) = 0.$$

Case II. $\mu = -\nu^2$, $\nu \geq 0$, gives rise to the Bessel differential equation of order zero:

$$R'' + \frac{1}{r}R' + \nu^2 R = 0$$

which has for its solution

$$R(r) = AJ_0(\nu r) + BY_0(\nu r)$$

where A and B are constants. Boundedness implies that $B = 0$, so that:

$$R(r) = AJ_0(\nu r).$$

Thus,

$$R'(r) = -A\nu J_1(\nu r)$$

$$R'(a) = -A\nu J_1(\nu a) = 0$$

which implies that $J_1(\nu a) = 0$ and determines the eigenvalues. The solution, then, to our original problem for $u(r, t)$ is

$$u(r, t) = e^{\lambda t} \sum_{j=1}^{\infty} A_j e^{-\kappa_j^2 t/a^2} J_0\left(\frac{\kappa_j r}{a}\right)$$

where κ_j is the j th root of $J_1(\kappa_j) = 0$. To determine A_j , we

use the initial condition along with the orthogonality of the Bessel function. From the initial condition

$$u(r, 0) = \sum_{j=1}^{\infty} A_j J_0\left(\frac{\kappa_j r}{a}\right)$$

we get

$$\int_0^{2\pi} \int_0^a r u(r, 0) J_0\left(\frac{\kappa_\ell r}{a}\right) dr d\theta = \sum_{j=1}^{\infty} A_j \int_0^{2\pi} \int_0^a r J_0\left(\frac{\kappa_j r}{a}\right) J_0\left(\frac{\kappa_\ell r}{a}\right) dr d\theta .$$

But since,

$$u(r, 0) = N_0 \delta(x, y)$$

this left hand integral is

$$\begin{aligned} \int_0^{2\pi} \int_0^a r u(r, 0) J_0\left(\frac{\kappa_\ell r}{a}\right) dr d\theta &= N_0 \int_0^{2\pi} \int_0^a r J_0\left(\frac{\kappa_\ell r}{a}\right) \delta(x, y) dr d\theta \\ &= N_0 J_0(0) \\ &= N_0 . \end{aligned}$$

Thus,

$$\begin{aligned} N_0 &= \sum_{j=1}^{\infty} A_j \int_0^{2\pi} \int_0^a r J_0\left(\frac{\kappa_j r}{a}\right) J_0\left(\frac{\kappa_\ell r}{a}\right) dr d\theta \\ &= A_\ell \frac{2\pi a^2}{2} J_1\left(\frac{\kappa_\ell a}{a}\right) \end{aligned}$$

so that, solving for A_ℓ we get

$$A_\ell = \frac{N_0}{\pi a^2 J_0(\kappa_\ell)} .$$

Note that for large values of t , since $\kappa_1 = 0$,

$$\lim_{t \rightarrow \infty} e^{-\lambda t} u(r, t) = \frac{N_0}{\pi a^2}$$

so that for large values of t , the bacteria are fairly uniformly distributed over the dish.

Incidentally, observe that the function

$$\begin{aligned} N(t) &= \int_0^{2\pi} \int_0^a u(r, t) r dr d\theta \\ &= \iint_A u dA \quad (\text{for simplicity}) \end{aligned}$$

satisfies:

$$N'(t) = \lambda N(t), \quad t > 0$$

$$N(0) = N_0$$

since;

$$\begin{aligned}
N'(t) &= \iint_A u_t dA \\
&= \iint_A (\Delta u + \lambda u) dA \quad (\text{from 3.1}) \\
&= \iint_A \operatorname{div}(\nabla u) dA + \lambda \iint_A u dA \\
&= \int_B \nabla u \cdot \nu ds + \lambda N(t) \\
&= - \int_B q \cdot \nu ds + \lambda N(t) \\
&= \lambda N(t)
\end{aligned}$$

since $q \cdot \nu = 0$ on the boundary. From this result we conclude that our model predicts the same total population as does the usual ordinary differential equations model.

By combining the methods of these two examples (i. e. Nomads and bacteria), one can also model the migration and propagation of geese and other migratory fowl.

V. ONE DIMENSIONAL URBAN GROWTH

The next example shows how one can model the growth of an urban area. For ease in presentation, we shall consider a one dimensional problem.

Suppose initially the total population is concentrated near the right end of the interval $0 \leq x \leq 1$, and the movement due to external causes is to the left. Suppose further that $\varphi - \psi = \lambda u$ and, to be more specific, that $\alpha = 1$ and that there is no immigration across the sides of the interval. Let us then consider the problem:

$$\text{D. E.} \quad u_t = \frac{\partial}{\partial x} (u_x + v(x)u) + \lambda u, \quad 0 < x < 1, t > 0$$

$$\text{B. C.} \quad u_x(0, t) + v(0)u(0, t) = 0 = u_x(1, t) + v(1)u(1, t), \quad t > 0.$$

$$\text{I. C.} \quad u(x, 0) = f(x)$$

where $v(x) = x^2$ (that is, there is no movement at $x = 0$ and the further away from $x = 0$, the faster the movement) and

$$f(x) = \begin{cases} A \left\{ \left[\frac{x-1}{\ell} \right]^2 - 1 \right\}^2 & 1-\ell \leq x \leq 1 \\ 0 & 0 \leq x \leq 1-\ell \end{cases}$$

with $A = 15N_0/8\ell$ where ℓ gives the width of the interval where the population is initially located. We have

$$\int_0^1 f(x)dx = A \int_{1-\ell}^1 \left\{ \left[\frac{x-1}{\ell} \right]^2 - 1 \right\}^2 dx = N_0$$

and

$$u_t = \frac{\partial}{\partial x} (u_x + v(x)u) + \lambda u$$

Let

$$u = e^{\lambda t} w.$$

Then

$$w_t = \frac{\partial}{\partial x} [w_x + v(x)w]$$

and the boundary conditions lead to

$$u_x + v(x)u = e^{\lambda t} [w_x + v(x)w] = 0 \Rightarrow w_x + v(x)w = 0 \quad \text{for } x=0,1.$$

This problem which is of the Sturm-Liouville type has no closed form solution so we examine the steady state solution for w . Let $t \rightarrow \infty$ so that $w_t = 0$ since there is no dependence on time in the equilibrium state.

Thus

$$(w' + vw)' = 0$$

Integrating gives

$$w' + vw = C$$

where C is constant. At $x = 0$,

$$w'(0) + v(0)w(0) = 0 \Rightarrow C = 0.$$

We now have the first order ordinary differential equation:

$$w' + vw = 0.$$

Using the integrating factor

$$\mu(x) = \exp \int_0^x v(s) ds ,$$

we have

$$\int_0^x v(s) ds \quad [w' + vw] = \left[e^{\int_0^x v(s) ds} w \right]' = 0$$

so that

$$w(x) = De^{-\int_0^x v(s) ds}$$

where D is constant. We note that:

$$\int_0^1 w_t dx = \int_0^1 [w_x + v(x)w]_x dx = 0.$$

$$\therefore \frac{d}{dt} \int_0^1 w(x, t) dx = 0 .$$

Thus,

$$\int_0^1 w(x, t) dx = \text{Constant} = \int_0^1 w(x, 0) dx = \int_0^1 f(x) dx$$

Let $t \rightarrow \infty$, then $w(x, t) \rightarrow w(x)$ and

$$\int_0^1 w(x) dx = N_0$$

so that

$$D \int_0^1 \frac{e^{-\int_0^x v(s) ds}}{e^{-\int_0^1 v(s) ds}} dx = \int_0^1 f(x) dx$$

$$\therefore D = \frac{\int_0^1 f(x) dx}{\int_0^1 \frac{e^{-\int_0^x v(s) ds}}{e^{-\int_0^1 v(s) ds}} dx} = \frac{N_0}{\int_0^1 e^{-x^3/3} dx}$$

Finally,

$$\lim_{t \rightarrow \infty} w(x, t) = w(x) = \frac{N_0}{\int_0^1 e^{-x^3/3} dx} e^{-\int_0^x v(s) ds}$$

so for large t , $w(x, t) \approx w(x)$ and

$$\therefore u(x, t) \approx e^{\lambda t} w(x) = e^{\lambda t} \frac{N_0}{\int_0^1 e^{-x^3/3} dx} e^{-x^3/3}.$$

For large values of t , we see that the population density is highest

around $x = 0$ and least around $x = 1$ as one would expect.

In a completely similar manner, one can derive equations governing the distribution of several populations. For two populations, the equations have the form:

$$u_t^{(1)} = \text{div}[\alpha^{(1)} \nabla u^{(1)} - v^{(1)} u^{(1)}] + \varphi_1(u^{(1)}, u^{(2)}) - \psi_1(u^{(1)}, u^{(2)})$$

$$u_t^{(2)} = \text{div}[\alpha^{(2)} \nabla u^{(2)} - v^{(2)} u^{(2)}] + \varphi_2(u^{(1)}, u^{(2)}) - \psi_2(u^{(1)}, u^{(2)})$$

where $u^{(1)}$ and $u^{(2)}$ refer to the population densities of the respective populations and the other functions have meanings completely similar to those already mentioned above.

VI. PREY-PREDATOR

Next we will deal with the case when a species of, say, soles swims into a species of, say, sharks. The sharks will feed on the soles available. We assume this all takes place over a very short time interval so that no reproduction takes place.

Assume the soles, denoted as species 1, is swimming from left to right (along the x-axis) with constant velocity v_1 . Assume the sharks, denoted as species 2, are swimming to the left with constant velocity $-v_2$. We make the example slightly unrealistic by assuming even after the species come together, they will continue on in the same direction as before the meeting with the same velocity. Further, we make the problem one dimensional.

Since the fish swim in schools we take $\alpha^{(1)} = \alpha^{(2)} = 0$. We assume that $\varphi_2 - \psi_2 = 0$ but that $\varphi_1 - \psi_1 = -\lambda u^{(1)} u^{(2)}$. Thus the problem to be solved takes the form:

$$\begin{aligned} \text{D. E.} \quad & u_t^{(1)} = -v_1 u_x^{(1)} - \lambda u^{(1)} u^{(2)} \\ & u_t^{(2)} = v_2 u_x^{(2)} \end{aligned}$$

$$\begin{aligned} \text{I. C.} \quad & u^{(1)}(x, 0) = f_1(x) \\ & u^{(2)}(x, 0) = f_2(x) \end{aligned}$$

We first solve for $u^{(2)}(x, t)$ by assuming a solution in the form

$$u^{(2)}(x, t) = f_2(x+a(t))$$

then

$$-v_2 u_x^{(2)} = -v_2 \frac{\partial}{\partial x} f_2(x+a(t)) = -v_2 f_2'(x+a(t))$$

and

$$u_t^{(2)} = a'(t) f_2'(x+a(t))$$

$$\therefore u_t^{(2)} - v_2 u_x^{(2)} = 0 = (a'(t) - v_2) f_2'(x+a(t))$$

so that we must have

$$a'(t) = v_2$$

Thus,

$$u^{(2)}(x, t) = f_2(x+v_2 t).$$

The method of characteristics now yields the solution for $u^{(1)}$.

From page 28,

$$u_y^{(1)} = -v_1 u_x^{(1)} - \lambda u^{(1)} u^{(2)}$$

now becomes

$$u_y^{(1)} + v_1 u_x^{(1)} = -\lambda f_2 u^{(1)}$$

with the initial condition:

$$u^{(1)}(x, 0) = f_1(x).$$

The characteristic equations are:

$$\frac{dx}{dt} = v_1 \quad \frac{dy}{dt} = 1 \quad \frac{du^{(1)}}{dt} = -\lambda f_2 u^{(1)} = -\lambda f_2 (x+v_2 y) u^{(1)}$$

and from the initial condition we have

$$y_0 = 0; \quad x_0 = s; \quad \text{and} \quad u_0^{(1)} = f_1(s).$$

$\therefore x = v_1 t + \varphi(s); \quad y = t + \psi(s)$ and the initial conditions give:

$$x = v_1 t + s \quad \text{and} \quad y = t.$$

Thus

$$\frac{du^{(1)}}{u^{(1)}} = -\lambda f_2 (x+v_2 y) dt = -\lambda f_2 (v_1 t + s + v_2 t) dt$$

so that

$$\log \frac{u^{(1)}(s, t)}{u^{(1)}(s, 0)} = -\lambda \int_0^t f_2((v_1 + v_2)\tau + s) d\tau$$

$$\therefore \frac{u^{(1)}(s, t)}{f_1(s)} = \exp \left\{ -\lambda \int_0^t f_2((v_1 + v_2)\tau + s) d\tau \right\}.$$

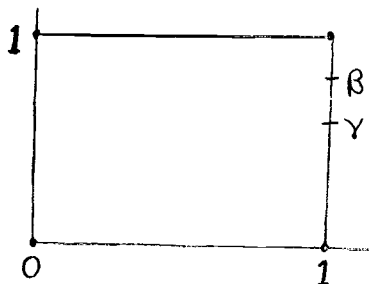
We have: $x = v_1 t + s; \quad y = t$ so that $s = x - v_1 y = x - v_1 t$. The final solution for $u^{(1)}(x, t)$ is

$$u^{(1)}(x, t) = f_1(x - v_1 t) \exp \left\{ -\lambda \int_0^t f_2(v_1 + v_2)\tau + x - v_1 t d\tau \right\}.$$

VII. SPAWNING SALMON

The final example will deal with salmon spawning, going to sea, returning, spawning, etc.

Consider the case of a square ocean, say $0 \leq x \leq 1$, $0 \leq y \leq 1$.



On part of the boundary, B , say $S = \{(x, y): x = 1, \gamma \leq y \leq \beta\}$, there are rivers where the salmon spawn and from there the fish diffuse into the ocean. After four years the mature salmon return to their spawning grounds. The equations that must be solved together with their boundary data are, therefore, the following: let T_1 , T_2 , T_3 , and T_4 be times, then

$$u_t = \operatorname{div}[\alpha \nabla u - \nu u] - \lambda u, \quad \lambda > 0.$$

Initially, we assume that $u(x, y, 0) = 0$ and for $(x, y) \in B - S$ we assume

$$(\alpha \nabla u - \nu u) \cdot \nu = 0.$$

We take $\lambda > 0$ to indicate that salmon will be lost, either by dying or by being eaten, during the time while at sea.

For, $0 < t \leq T_1$, we take

$$-(\alpha \nabla u - \nu u) \cdot \nu = \varphi \text{ on } S$$

where φ gives the rate at which the young salmon are entering the sea during this time interval.

During the interval $T_1 < t \leq T_2$,

$$-(\alpha \nabla u - \nu u) \cdot \nu = 0 \text{ for } (x, y) \in S$$

which means that no more fish are entering the sea. Furthermore, during the interval $0 < t \leq T_2$, $\nu(x, y, t) = 0$ since it is assumed that the salmon simply diffuse in all directions.

Finally, for $T_2 < t \leq T_3$, the salmon swim to the region S at velocities allowing them to arrive at S . The differential equation becomes

$$u_t = -\text{div}(\nu u) - \lambda u.$$

On S we need to keep track of those entering the river systems, say $\int_S \nu u \cdot \nu ds$. Thus, during the interval $T_2 < t \leq T_3$

$$N_0 = \int_{T_2}^{T_3} \int_S \nu u \cdot \nu ds$$

will have entered.

The spawning which takes place during $T_3 < t \leq T_4$ yields a population, $N(t)$, determined from

$$N'(t) = \mu N(t)$$

$$N(T_3) = N_0$$

At time $t = T_4$, the N individuals distributed uniformly along S will begin to re-enter the ocean which is assumed to have zero population density and the process repeats itself.

As an example of how this works, consider the following one-dimensional model.

We have first to solve:

$$(D. E.) \quad u_t = u_{xx} - u$$

$$(B. C.) \quad \begin{aligned} u_x(0, t) &= 0 \\ u_x(1, t) &= \begin{cases} 10, & 0 \leq t \leq 1 \\ 0, & 1 < t \leq 2 \end{cases} \end{aligned}$$

$$(I. C.) \quad u(x, 0) = 0;$$

and finally

$$u_t = (vu)_x - u \quad 2 < t \leq 3$$

u continuous

$$v(x) = 1 - x$$

and

$$N_0 = \int_2^3 vu(1, t) dt$$

$$N'(t) = 5N(t), \quad N(3) = N_0.$$

To solve this system we start with the time interval $0 < t \leq 1$
and solve the problem:

$$(D. E.) \quad u_t = u_{xx} - u$$

$$(B. C.) \quad u_x(0, t) = 0$$

$$u_x(1, t) = 10$$

$$(I. C.) \quad u(x, 0) = 0.$$

Let $u = e^{-t}v$, then the problem for $v(x, t)$ is:

$$(D. E.) \quad v_t = v_{xx}$$

$$(B. C.) \quad v_x(0, t) = 0$$

$$v_x(1, t) = 10e^t$$

$$(I. C.) \quad v(x, 0) = 0.$$

The function $V(x, t) = 5x^2 e^t$ satisfies the boundary conditions in the
problem for $v(x, t)$. Define:

$$w(x, t) = v(x, t) - V(x, t)$$

The problem for $w(x, t)$ is:

$$(D. E.) \quad w_t - w_{xx} = -(5x^2 - 10)e^t$$

$$(B. C.) \quad w_x(0, t) = 0$$

$$w_x(1, t) = 0$$

$$(I. C.) \quad w(x, 0) = -V(x, 0) = -5x^2$$

We break this problem into two parts and get the solution for $w(x, t)$ by superposition. We first solve:

$$(D. E.) \quad Z_t = Z_{xx}$$

$$(B. C.) \quad Z_x(0, t) = 0 = Z_x(1, t)$$

$$(I. C.) \quad Z(x, 0) = -5x^2$$

and get for its solution

$$Z(x, t) = \sum_{n=0}^{\infty} a_n e^{-\lambda_n^2 t} \cos \lambda_n x, \quad \lambda_n = (n\pi)$$

where

$$a_m = \begin{cases} -\frac{5}{3}, & m = 0 \\ \frac{10(-1)^n}{(m\pi)^2}, & m \geq 1 \end{cases} .$$

Next we must solve:

$$(D. E.) \quad z_t = z_{xx} - (5x^2 - 10)e^t$$

$$(B. C.) \quad z_x(0, t) = 0 = z_x(1, t)$$

$$(I. C.) \quad z(x, 0) = 0.$$

For its solution we get

$$z(x, t) = \sum_{n=0}^{\infty} \alpha_n(t) \cos(\lambda_n x), \quad \lambda_n = (n\pi)$$

where

$$\alpha_n(t) = \begin{cases} (a_0 + 10)[e^t - 1], & n = 0 \\ \frac{a_n}{1 + \lambda_n^2} [e^t - e^{-\lambda_n^2 t}], & n \geq 1. \end{cases}$$

We now have $z(x, t)$ and $Z(x, t)$. Thus;

$$w(x, t) = z(x, t) + Z(x, t)$$

so that

$$v(x, t) = z(x, t) + Z(x, t) + V(x, t)$$

and finally,

$$u(x, t) = e^{-t} \{z(x, t) + Z(x, t) + V(x, t)\}.$$

For the time interval $1 < t \leq 2$ we must solve the problem:

$$(D. E.) \quad u_t = u_{xx} - u$$

$$(B. C.) \quad u_x(0, t) = 0 = u_x(1, t)$$

(I. C.) u continuous across $t = 1$.

That is,

$$\begin{aligned} u(x, 1) &= \frac{1}{e} \{z(x, 1) + Z(x, 1) + V(x, 1)\} \\ &= F(x) \quad (\text{for simplicity in handling}). \end{aligned}$$

For the solution, we let $u(x, t) = W(x, t) \cdot e^{-t}$, then $W(x, t)$ must solve the more familiar problem

(D. E.) $W_t(x, t) = W_{xx}(x, t)$

(B. C.) $W_x(0, t) = 0 = W_x(1, t)$

(I. C.) $W(x, 1) = eF(x)$.

The solution for $W(x, t)$ is found by the usual method of separation of variables. We get

$$W(x, t) = \sum_{n=0}^{\infty} c_n e^{-\lambda_n^2 t} \cos(\lambda_n x)$$

where

$$c_m = \begin{cases} \int_1^2 eF(x) dx, & m = 0 \\ 2e^{\lambda_m^2 + 1} \int_1^2 F(x) \cos(\lambda_m x) dx, & m \geq 1. \end{cases}$$

The solution for $u(x, t)$ in $1 < t \leq 2$ is

$$u(x, t) = e^{-t} W(x, t) = \sum_{n=0}^{\infty} c_n e^{-(\lambda_n^2 + 1)t} \cos(\lambda_n x) .$$

For the interval of time, $2 < t \leq 3$, we have the problem:

$$(D. E.) \quad u_t = (vu)_x - u, \quad v(x) = 1 - x$$

u continuous across $t = 2$.

u continuous across $t = 2$ implies that

$$\begin{aligned} u(x, 2) &= \sum_{n=0}^{\infty} c_n e^{-(\lambda_n^2 + 1)2} \cos(\lambda_n x) \quad [\text{from previous work}] \\ &= G(x) \quad (\text{for simplicity in handling}). \end{aligned}$$

The method of characteristics now yields the solution:

$$u(x, t) = e^{-2(t-2)} G(1+(x-1)e^{2-t})$$

The spawning which takes place produces

$$N(t) = e^{-15} N_0 e^{5t}$$

individuals, where

$$N_0 = \int_2^3 vu(1, t) dt.$$

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